# THE IMPACTS OF ENVIRONMENTAL WARMING ON THE ECOLOGY OF BRITISH DRAGONFLIES AND DAMSELFLIES

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by

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# ABSTRACT

The evidence for rapid contemporary climate change is now irrefutable and regardless of whether or not this change is of anthropogenic origin the academic community has been presented with an opportunity to investigate the responses of the world's biota to changing temperature. I focus on three aspects of the ecology of Odonata: (i) historical trends from database records, (ii) geographical variation in morphology in relation to range location and (iii) the interaction between Odonata and their biotic and abiotic environment.

Historical datasets – I demonstrate that the Odonata have shown a strong signal of advancing phenology through an analysis of historical records of sightings between 1960 and 2005. This is the first time such a shift in phenology has been demonstrated in an aquatic taxon and this shift is comparable to those observed in terrestrial taxa. The same database has also been used to evaluate distributional shifts in the Odonata. I show that the methods used in published studies of distributional changes that use unstructured datasets contain potential sources of error and make recommendations as to how these errors can be reduced. Finally, I investigate the extent to which distributional changes in Odonata will affect the use of this taxon as an indicator of water quality within the RIVPACS scheme. This demonstrates that artefacts can be introduced into assessments of water quality through not taking into account climate-induced range shifts as a contributing factor to changing species distributions.

Variation in morphology – In the first of two pairs of studies I demonstrate that the varying rate at which three species are expanding their range in the UK is related to the degree of exaggeration in dispersal morphology at the range margin relative to the core of the range. The species expanding at the greatest rate demonstrated the greatest increase in dispersal-related traits at the expanding range margin. Using specimens of *Calopteryx splendens* that were collected as part of this study I give evidence for a variation in immune function between two populations in the south and north of England. In the second pair of studies I show that two sympatric damselfly species exhibit varying relationships between morphological traits and latitude. The species which is expanding its range shows classic latitude-size patterns whereas the species that is not expanding does not. Further to this I show that the wings of *Coenagrion puella* vary in shape towards the range margin in Scotland. I suggest that this may be the result of increased developmental instability close to the species' thermal limits.

Odonata and the environment – As well as the broad historical changes in distributions that have been detected using databases of sighting, fine-scale research is required to describe the characteristics of the environment within which Odonata live. I test a number of hypotheses concerning the interactions between Odonata including the ability of different aspects of the environment to predict odonate community structure and the use of botanical communities as indicators of the nature of water bodies. Finally I examine the role of Odonata as a predator within the context of the invertebrate community in making predictions concerning the future of aquatic communities under varying hydroperiods. This demonstrates that vertebrate predators are susceptible to decreases in hydroperiod while dytiscid beetles, which exhibit the same dietary preferences, are ubiquitous in the aquatic environment and are unaffected by drought.

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Over the past couple of years I have been to a range of conferences and courses at which I have been constantly stimulated and interested. All those talks at Valencia, Plymouth, Windermere, St Andrews, York, Glasgow, Oxford and Silwood Park were not only fascinating in their own right but also provided me with the ideas and skills I required to make the most of my studies. In particular Mick Crawley's course on ecological modelling using R early on in my PhD equipped me with a perspective on data analysis and modelling that has made my subsequent work far more efficient than it otherwise would have been.

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# *Chapter 1. Introduction*

## 1.1. Climate change: causes and consequences

### 1.1.1. Evidence for current climate change

The premise of this work is that there is ongoing climatic change. The evidence for this is unequivocal (Karl and Trenberth, 2003, IPCC, 2007). However, it is important to bear in mind some of the more subtle aspects of this general trend, including regional climate processes (Pielke Sr, 2005), variations in climate change between seasons (Vogelsang and Franses, 2005), the range of climatic variables that are going to be altered along with temperature (IPCC, 2007) and the wider temporal context within which the current warming occurs (Adams et al., 1999).

The evidence for the current phase of environmental warming is easy to obtain. Any interested party can go to the UK's Met Office web site and see the graphs for themselves or even download the data from which they have been calculated and create their own (Figure 1.1). This kind of openness with data is unusual in science but certainly helps to reassure the public about the clear message that is conveyed.

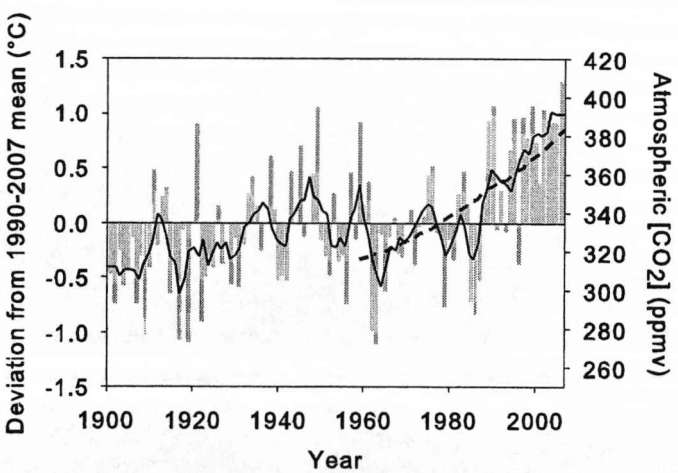


**Figure 1.1 – Variation in temperature from 1990-2007 expressed as deviation from the mean temperature of that period[1]. Solid line represents a moving average with a sampling proportion of 0.05 and dotted line represents atmospheric CO2 concentration as recorded at Mauna Loa observatory[2].**

[1] data available from http://hadobs.metoffice.com/hadcet/ssn_HadCET_mean.txt
[2] data available from http://cdiac.ornl.gov/ftp/trends/co2/maunaloa.co2

While a large proportion of the general public believes that there is a lack of consensus over the cause of this phase of warming, this is simply not true (IPCC, 2007). However, there is a small, vociferous minority that continues to voice arguments against a substantial anthropogenic effect, some of whom are willing to put their money where their mouths are (Giles, 2005). The anthropogenic effect comes from greenhouse gases, including carbon dioxide (see data in Figure 1.1), changes in land-use (particularly deforestation) and the release of aerosols (IPCC, 2007).

A variety of natural oscillations also contribute to climatic variation including 11-year cycles in solar radiation (Foukal et al., 2006), the North Atlantic Oscillation (NAO) and the El Nino-Southern Oscillation (ENSO). These latter climate oscillations are predicted to cause a slowdown in global warming by offsetting anthropogenic factors for the next decade (Keenlyside et al., 2008). The complexity inherent within the system provides a number of bolt-holes for those who wish to question the accuracy of both the detection of the current trend and future projections.

### 1.1.2. Climate change and man

The impacts of changing climate on human society are of great significance in both scientific and popular publishing worlds. Increasing environmental temperature and variations in precipitation are projected to alter freshwater availability, leading to conflict over existing freshwater reserves both for drinking water and continued irrigation of increasing areas of agricultural land (Vorosmarty et al., 2000). The continued melting of the Arctic ice could hinder or stop the Gulf Stream, which is responsible for the mild climate in Europe (Bryden et al., 2005), making European climates more comparable to those at similar latitudes in North America. Sea-level rise will cause vast coastal flooding, a potential catastrophe in low-lying areas such as the Mediterranean coastline and south and south-east Asia (Nicholls et al., 1999).

However, it is important that we do not begin to tie all the world's ailments to climate change. The issues associated with water availability will be impacted just as greatly, if not to a greater extent, by man's over-exploitation of both lentic and lotic water bodies. There have also been a large number of articles predicting increases in tropical diseases in temperate zones as a result of global warming which simply are not borne out by scientific research (Reiter, 2001, Reiter et al., 2004). The impacts of sea-level rise are also predicted to be modulated substantially by the construction of coastal defences and other socioeconomic factors (Nicholls, 2004). It is important that science steers clear of the politicization of the subject.

### 1.1.3. Climate change and the natural world

The kind of errors highlighted by Paul Reiter and colleagues make it obvious that we need a greater understanding of how the world's biota is responding to climate change in order to fully understand the implications for mankind. The potential impact of climate change on the global biota is substantial, with 15-37% of a broad range of sampled species predicted to go extinct (Thomas et al., 2004). A similarly wide range of taxa have been shown to be responding to environmental change in the same way, emphasizing the globally coherent "footprint" of climate change (Parmesan, 2006, Parmesan and Yohe, 2003, Walther et al., 2005, Root et al., 2003).

That climate change has recently (in geological timescales) contributed to the widespread extinction of the Pleistocene megafauna (Barnosky et al., 2004) but not the invertebrate fauna (Coope, 1995b) suggests a variability in susceptibility to the current phase of global change. Ideally, the most sensitive taxa would be used to test for the effects of this factor. However, the amenity of invertebrates (particularly insects) to genetic, physiological, laboratory and field studies makes this group a far more attractive prospect for developing and testing detailed hypotheses concerning their responses to climate change.

In this work I set out to investigate the impacts that environmental warming is having on the ecology of the Odonata. In the rest of this introduction I shall briefly summarise the approaches taken and the rationale behind the various studies that were conducted. I shall refrain from extensive referencing in this section and, instead, refer the reader to the relevant sections in the literature review, Chapter 2.

## 1.2. Thesis structure

### 1.2.1. Literature review

In Chapter 2 I establish the background literature on the topic, highlighting contributions to the field from disciplines ranging from molecular ecology and physiology through to macroecology and large-scale field projects. The broad range of approaches help us not only to observe the extent of the real-world impact of climate change on this group but also to understand the proximate causes of those impacts, thereby making the body of research both relevant and precise.

From here the thesis can be divided into three discrete, though related, sections, each of which contain a number of studies. These comprise (i) an analysis of past records of sightings of Odonata

in the UK to assess past responses to climate change, (ii) field work designed to evaluate morphological and physiological variation at range margins and (iii) an analysis of ponds as a habitat both at a habitat- and landscape-level.

### 1.2.2. Section 1 – Analysis of historical records

I investigate past trends in odonate phenology in Chapter 3 using a historical database of sightings that is maintained by the British Dragonfly Society (BDS). Unlike data on butterflies which have been collected in the UK as part of the methodical Butterfly Monitoring Scheme, the BDS database showed substantial bias towards lower latitudes and later time periods. Such bias had led some members of the BDS to question whether there was anything of value to be gained from analysing the data. However, having adapted existing techniques used to control for data that are not collected methodically, I found a significant signal of advancement in the leading edge of the flight period. The extent of the detected shifts was comparable with phenology studies in other taxonomic groups.

However, the study was more than simply a confirmation that Odonata are responding to climate change by emerging earlier, although this is of interest in its own right. The fact that Odonata are an aquatic group was the first confirmation that aquatic as well as terrestrial taxa are responding to environmental warming in a similar way. I also demonstrated that the latter portion of the emergence period does not appear to be so predictable. Species varied in their responses to climate change, exhibiting (i) an advance to track that of the preceding edge of the flight period, (ii) no change, or (ii) a lengthening of the flight period with the trailing edge mirroring the change in the preceding edge. Such variation between species may have substantial impacts on population biology if the length of the flight period – and, therefore, the reproductive period – varies in length between species. This merits further study.

Also of interest in analysing long-term records is the issue of changing distributions with time. However, just as I began my analysis of range shifts in the data, the results of a similar study were published (Hickling et al., 2005). On closer inspection, however, this particular study makes a number of errors in its analysis of the records, including looking for range shifts in species that have already reached the northern coast of Scotland, the inclusion of very rare species whose distributions are likely not determined by climate and questionable methods used to control for the biases mentioned above. Just as I was preparing to correct their mistakes, a second paper was published in which those errors were largely remedied (Hickling et al., 2006).

The change in methods between the two studies highlighted the absence of an established methodology for the analysis of historical databases in which records are heterogeneously distributed. Chapter 4 describes an attempt on my part to review the methods used in such analyses with the BDS database as a testbed. The reviewed methods have resulted in a range of high-profile publications but have never been compared to assess variations in their results.

Finally in this section, the implications of climate-induced range shifts were considered beyond the ecological sphere. Macroinvertebrates play a role in the monitoring of water quality based on the River Invertebrate Classification Scheme (RIVPACS) within which each family is allocated a score according to its tolerance to pollution. The fact that the probability of the presence of Odonata in a given habitat is determined by something more than the level of pollution in the water body violates the assumptions of the RIVPACS scheme. In Chapter 5 I set out to evaluate the impacts of changing distributions on the validity of biological water quality metrics.

### 1.2.3. Section 2 – Climate and morphological variation

The next section takes us away from past records of Odonata and the detection of past trends and considers the ecological implications of morphological variation which occurs as a result of climate. I conducted two studies during the summers of 2006 and 2007 to evaluate this variation in multiple species. The first study described in Chapter 6 involved a comparison of size and dispersal-related traits between core and marginal populations. The results suggest strong variation between these pairs of sites in three species of Zygoptera with the species exhibiting the greatest geographic range shift possessing the most exaggerated trait differences.

An aside to the study described in Chapter 6 was the discovery of variation in the size of wing spots in the banded demoiselle, *Calopteryx splendens*, described in Chapter 7. Such variation in a physiological trait is linked to climate through a pair-wise comparison of sites and is implicated as a potential ecological determinant of geographical range. This is further supported by a comparison of the thermal environment at the species' range margin in the UK and in Scandinavia. While a relatively short note, this chapter provides a result which is novel, relevant and (at least in statistical terms) significant, and that merits further research.

The methods used in the study described in Chapter 6 were aimed at minimising the impact of sampling on the population under investigation. This was done by anaesthetising individuals at low temperatures before making measurements and subsequently releasing those individuals. During the course of that study, a number of methodological problems were identified which led to a

similar, refined study being conducted in the following summer which is described in Chapter 8. This study compared two species of Zygoptera rather than three but took place over a latitudinal cline of seven or eight sites rather than the pairwise comparison used in Chapter 7. The aim of this study was two-fold: (i) to quantify latitudinal variation in morphology as a proxy for variation with climate, and (ii) to assess the relative contributions of climate and the range expansion that is apparently occurring in one of the two species to that variation in morphology.

Like the data from Chapter 6 which spawned Chapter 7, Chapter 8 also begat a study on examining variation in wings which is described in Chapter 9. However, rather than using wing measurement as an indicator of physiological state, I used the shape of the wings themselves as an indicator of variation between populations. By employing geometric morphometrics, I investigate what happens to the wing shape of *Coenagrion puella* as it approaches its range margin in mid-Scotland.

### 1.2.4. Section 3 – Odonata and the pond landscape

The thesis then takes a step back in terms of scale to include not only the populations within the habitats but also the relationship between Odonata and their habitat. Chapter 10 investigates this by examining a large number of pond surveys in which a range of chemical, botanical and hydrogeological variables were recorded alongside the recording of Odonata identified to species. The sample size of this dataset is an order of magnitude larger than previous analyses and confirms a number of associations which have been illustrated previously as well as highlighting some that have not and questioning those that have come before. Other hypotheses tested include the notion that botanical communities are indicative of certain properties of water bodies, that certain variables correlate with odonate diversity and that Odonata are indicators of general species richness.

The variation in susceptibility of different components of the biota to climate change raises a number of questions regarding the future composition and structuring of communities that currently contain more sensitive taxa. In aquatic communities where they are present, fish are considered to be the principle taxon which is responsible for structuring the rest of the community (Bendell and McNicol, 1995). However, under certain conditions (principally short hydroperiods, high temperatures and low oxygen levels), fish are replaced by invertebrates. This change in community structure in freshwaters along a water permanence gradient has been thoroughly described (Wellborn et al., 1996). In Chapter 11 I examine the role of Odonata as top predators in aquatic ecosystems, comparing their trophic niche with that of other invertebrate predators and a number of fish species. The results show that it is not Odonata but Coleoptera (specifically

Dytiscidae) which are likely to take over from fish as top predators in aquatic ecosystems, lending a theoretical basis to the pattern that has been seen elsewhere (Wissinger et al., 2006).

Since the individual thesis chapters contain discussions of the broader relevance of the results contained therein, the thesis is concluded in Chapter 12 with a brief summary of the key results followed by a discussion of some relevant topics that are not covered elsewhere. I have not included taxonomic authorities in the body of the text. For Odonata that are mentioned I have provided an appendix with the relevant authorities. For other species I have not provided the authority but I have given additional taxonomic information at the first occurrence of each species name in each chapter.

# *Chapter 2. The effects of environmental warming on Odonata: a review*

## 2.1. Abstract

Climate change brings with it unprecedented rates of increase in environmental temperature, which will have major consequences for the earth's flora and fauna. The Odonata represent a taxon that has many strong links to this abiotic factor due to its tropical evolutionary history and adaptations to temperate climates. Temperature is known to affect odonate physiology including life-history traits such as developmental rate, phenology and seasonal regulation as well as immune function and the production of pigment for thermoregulation. A range of behaviours is likely to be affected which will, in turn, influence other parts of the aquatic ecosystem (primarily through trophic interactions). Temperature may influence changes in geographical distributions, through a shifting of species' fundamental niches, changes in the distribution of suitable habitat and variation in the dispersal ability of species. Finally, such a rapid change in the environment results in a strong selective pressure towards adaptation to cope and the inevitable loss of some populations (and, potentially, species). Where data are lacking for odonates, studies on other invertebrate groups will be considered. Finally, directions for research are suggested, particularly laboratory studies that investigate underlying causes of climate-driven macroecological patterns.

## 2.2. Introduction

The causes of the current phase of environmental warming have received a great deal of attention both from within the scientific literature and in the public sphere. The main driver behind contemporary warming is now considered to be anthropogenic, mainly because of the unprecedented rate of increase in temperature (Mann, 2007, Karl and Trenberth, 2003). However, regardless of the causes of these variations in temperature, the current state of climatic flux provides an important opportunity to conduct natural experiments into the impacts of varying temperature on the world's biota.

Quaternary studies have shown using climate proxies that flora and fauna have survived rapid climate fluctuations in the past (Davis and Shaw, 2001, Adams et al., 1999, Coope, 1995a, Coope, 1995b). It has been reasoned that, since all extant species must have had progenitors who survived those past fluctuations, all extant species must possess adaptations that would enable them to cope with the same hurdles again (Balmford, 1996). This is supported by the range of biological responses that have been documented (Parmesan, 2006).

The Odonata have a long history in the fossil record relative to other orders, with fossils present from the Lower Permian (Wootton, 1981). This fact, coupled with a range of adaptations which have enabled them to colonise temperate and subarctic habitats from their tropical origins (Pritchard and Leggott, 1987), make them ideally suited to surviving current climate change. This review will consider the impact of environmental warming on a range of aspects of odonate biology to investigate how true this intuitive assumption may be.

A variety of factors make the Odonata an ideal model taxon for the investigation of the impacts of environmental warming and climate change. These include: (1) a tropical evolutionary origin potentially leading to limitations of distribution by temperature, (2) the use of temperature in seasonal regulation, (3) high local abundances in some species, making fieldwork involving ecological sampling not only feasible but relatively straightforward, (4) a long history of scientific research into both their ecology and behaviour, and (5) extensive amateur recording resulting in large historical databases of sightings.

This review is arranged hierarchically according to levels of organisation, beginning with physiological impacts of temperature on life-history parameters and thermoregulation. Then species interactions within habitats are discussed before moving onto the distributions of Odonata and their habitats in the landscape. Finally, the influence of temperature on broader topics such as evolution and extinction risk is considered.

## 2.3. Life histories

### 2.3.1. Development

The intuitive link between increasing temperature and increasing developmental rate has been illustrated in a range of laboratory experiments in larvae (Pritchard et al., 2000, Van Doorslaer and Stoks, 2005, Pickup and Thompson, 1990, Krishnaraj and Pritchard, 1995) and in the egg stage (Masseau and Pilon, 1982). The Odonata are unique in being the only taxon of aquatic insects which exhibits solely negative relationships between egg development time and temperature (Pritchard et al., 1996). The population model developed by Crowley et al. (1987) considered a direct effect of temperature on development rate only in the egg stage, with indirect effects of temperature via feeding rates in 'small' and 'large' larval classes (as demonstrated by Lawton et al., 1980). Subsequent work has not only supported this indirect effect, but also illustrated that a direct effect is present (Van Doorslaer and Stoks, 2005).

Population-level adaptations in developmental rate to local thermal regimes have been demonstrated in *Argia vivida*, a species found in a range of temperature environments (Leggott and Pritchard, 1985). This adaptation needs to be borne in mind otherwise predictions of future growth rates under environmental warming will underestimate true values. A range of studies have pointed to high thermal thresholds for development compared to other invertebrates, both in the egg – 11.25°C in *Argia vivida* (Leggott and Pritchard, 1985) and 12°C in *Coenagrion puella* (Waringer and Humpesch, 1984) – and larvae – 8°C in *Ischnura elegans* (Thompson, 1978c). Species-level adaptation to varying hydroperiod has been proposed as a mechanism by which growth rate has been accelerated in *Lestes* spp. (De Block et al., 2008a). This is particularly pronounced in *L. dryas*, which inhabits vernal pools (with annual drying).

### 2.3.2. Temperature and photoperiod

Responses to temperature in nature are potentially complicated by a range of species-specific responses to changing photoperiod (summarised in Corbet, 1999, p.288). Photoperiodic cues are thought to play a role in regulating larval development (Norling, 1984b) and, as such, influence the temperature-developmental rate relationships described above. In order to properly consider the effects of either variable, the other needs to be accounted for.

The effect of photoperiod on development was first observed in *Anax imperator* (Corbet, 1955, Corbet, 1956a) and early experiments showed that a longer photoperiod accelerated development on *Tetragoneuria cynosura* (Jenner, 1958, Lutz and Jenner, 1960, Lutz, 1963). The same experimental paradigm has been used in many studies to examine effects of temperature and photoperiod (Corbet et al., 1989, Sawchyn and Church, 1973). However, it was not until a tightly controlled experiment by Johansson & Rowe (1999) on *Lestes congener* that an increase in developmental rate (moult frequency) was unequivocally demonstrated. Such an increase in developmental rate was not mirrored by an increase in growth rate, a finding confirmed in a study on *Lestes viridis* (De Block and Stoks, 2003). Both studies showed large effects of photoperiod on size and age at emergence.

Critical photoperiods – the light: dark ratio required to elicit a response such as diapause – have been shown to vary with latitude in a range of insects (Danilevskii, 1965), as well as in odonates (Norling, 1984a). This variation has also been shown in *Aquarius paludum* (Hemiptera: Gerridae), to occur over time at the same location, with the suggestion that increasing environmental temperature may be the cause (Harada et al., 2005).

In addition to a photoperiodic modulation of temperature-development relationships, low temperatures can also influence photoperiodic responses. *Enallagma hageni*, a northern species, was shown to exhibit photoperiodic responses at lower temperature than *Enallagma aspersum*, a southern species (Ingram and Jenner, 1976).

### 2.3.3. Diapause

The high incidence of diapause in Odonata compared to other taxa has been taken as evidence for a tropical origin and invasion of temperate regions (Pritchard and Leggott, 1987). Diapause induction and cessation have been shown to be elicited by photoperiod and temperature in a range of odonates (Corbet et al., 1989, Sawchyn and Church, 1973, Pritchard, 1989, Ingram, 1975, Corbet, 1956b, Boehms, 1971). These studies provide good evidence for Norling's (1984b) two-stage model of diapause induction. The evolution of diapause as a mechanism for colonising temperate regions from the tropics has been implicated in speciation processes in American taxa (Pritchard, 2008).

The reliance of diapause on low temperatures may place some species at risk if certain temperature thresholds are passed during environmental warming. Diapause induction avoids periods of low energy availability for ectotherms and low food availability. If diapause induction fails due to high temperatures, developmentally active ectotherms may suffer increased mortality (Harrington et al., 2001). Current development models do not include temperature as a factor affecting diapause (Braune et al., 2008).

### 2.3.4. Phenology

The study of phenology has received rigorous attention in the past decade and has shed much light on the responses of invertebrates (Roy and Sparks, 2000), vertebrates (Crick and Sparks, 1999) and plants (Fitter and Fitter, 2002) to changing temperatures. A recent meta-analysis of a range of taxa (though not including Odonata) gave an estimate of advancement in spring phenology of 2.8 days·decade$^{-1}$ (Parmesan, 2007). British Odonata follow the same pattern in response to warming, with the flight periods beginning progressively earlier in the year (Hassall et al., 2007). Hassall et al. demonstrate that the odonate phenological response is species specific, being modulated by the presence of a diapause stage in the egg. While the leading edge of the flight period advanced, the trailing edge exhibited a range of responses between tracking of the leading edge and regressing to later in the year.

Subsequent analyses of more detailed, though briefer, time series have suggested that different temperature variables have different effects on phenology (Dingemanse and Kalkman, 2008). At still

higher resolution, Richter et al. (2008) produced a temperature-sum model to describe the emergence of *Gomphus vulgatissimus*, which performed well when checked using field data. These three studies offer strong support for the role of temperature in determining phenology.

Patterns of emergence vary spatially and temporally between species. In addition to the distinction between spring and summer species (Corbet, 1954), particular species may exhibit multiple peaks in emergence. In some cases this may be due to simple bi- or multivoltinism. Alternatively, an overlap of generations within a population close to a voltinism threshold can result in cohorts exhibiting different voltinisms emerging at different times during the same year (see the appendix of Corbet et al., 2006 for a thorough review). Models have predicted that species will substantially increase the rate at which generations are produced (Braune et al., 2008).

However, multiple emergence peaks also occur in species with a single voltinism class. An example is *Pyrrhosoma nymphula* in northern Scotland (Corbet and Harvey, 1989), which exhibits two peaks in emergence within a semivoltine life cycle due to larvae overwintering in one of two instars. While there are multiple explanations for variations in growth rate, temperature is often an important factor and increases in temperature would be expected to synchronise this emergence pattern into a single peak while potentially turning synchronised emergence events into multiple peaks.

Studies into the ecological impacts of changing phenology have shown that decoupling of trophic interactions is possible (Winder and Schindler, 2004, Harrington et al., 1999, Walther et al., 2002). Such decoupling has been reported for birds feeding on larval Lepidoptera (Both and Visser, 2005) and *Daphnia* grazing on diatoms (Winder and Schindler, 2004). It is often assumed that odonates are generalist predators and so phenological mismatching will not directly affect their trophic interactions. However, brief peaks in the abundance of prey species may provide a vital source of food when a high rate of food intake is required, e.g. during the early pre-reproductive period. Small odonate larvae are reliant on a relatively small range of prey due to limitations on the size of prey that can be captured (Thompson, 1978b) resulting in a potential reliance on particular species.

Climate-induced variations in tipulid emergence on blanket bogs (which can form important odonate habitat) have been linked to the population dynamics of *Pluvialis apricaria* (Aves), a moorland wading bird (Pearce-Higgins et al., 2005). It might be expected that prey diversity would be low at higher latitudes and altitudes and that this would necessitate higher interaction strengths between the few remaining species in food webs. It would be worthwhile to investigate the diets of

odonates at low prey diversities to establish whether such reliance (and, therefore, a risk of trophic decoupling) is present.

## 2.4. Thermoregulation

Thermoregulation and the temperature biology of odonates have received extensive coverage elsewhere (May, 1991, May, 1976). As a result, I shall briefly summarise the research on the different areas of thermoregulation.

### 2.4.1. Pigmentation

Physiological colour change is a common feature of thermoregulation in Odonata (Corbet, 1980) and is unusually common in Odonata compared to other taxa in central Europe (Sternberg, 1996). It has been suggested that populations of some species vary in colouration with latitude to enhance the absorbance of heat in cooler regions, e.g. *Orthetrum cancellatum* (Hilfert-Rüppell, 1998). As well as varying with latitude, pigmentation can also vary with temperature throughout the day, e.g. *Argia vivida* (Conrad and Pritchard, 1989) and *Aeshna caerulea* (Sternberg, 1996). This hypothesis is supported further by the observation that the abdomen of *Ischnura elegans*, which is active at relatively low temperatures, is 90% black compared to 40% for *Coenagrion puella* and *Enallagma cyathigerum*, which are not active at lower temperatures (Hilfert-Rüppell, 1998). Such a pattern could be investigated more thoroughly using modern spectroscopic techniques.

Although this indirect evidence was not at first supported by experimental work (e.g. Veron, 1974), Sternberg (1990, 1989) showed that there was an appreciable impact of colouration on body temperature in some Anisoptera. Evidence for a communicative function for body colouration has been equivocal at best whereas a thermoregulatory role for melanic forms has been shown in other taxa (Sternberg, 1996). In a carefully controlled experiment Sternberg (1996) showed conclusively that colour phase impacted on the rate of heat gain. He measured the rate of warming in different colour phases exposed to the same source of radiant energy as well as comparing the amount of time taken to reach thermal limits for behaviours, viz. eye-cleaning, wing-whirring and take-off, during warming.

Sternberg (1996) proposed that the higher frequency of androchrome females at lower latitudes may be due to the need for greater thermoregulation. He also speculated that this form of thermoregulation partly contributes to the difference between the bimodal diurnal activity patterns of *Aeshna* females which cannot thermoregulate through colour change and the unimodal diurnal activity patterns of *Aeshna* males that are capable of colour change.

### 2.4.2. Basking

The use of solar radiation in thermoregulation has been documented extensively in odonates in the field (e.g. Hilfert-Rüppell, 1998). Laboratory experiments have also confirmed the effectiveness of 'obelisking' (May, 1976) in reducing heat absorption. Field experiments have shown that *Aeshna caerulea* can use its wings to effectively increase body temperature by creating a 'glasshouse' (Sternberg, 1990).

### 2.4.3. Microhabitat use

Although habitat requirements of Odonata are relatively poorly understood, there is strong evidence for selection of warmer pools (with high humic content, shallowness and a dark benthos) as oviposition sites in the boreal *Aeshna caerulea* (Sternberg, 1997). The colonisation of North America by the genus *Argia* has been attributed to a selective use of geothermally heated streams (Pritchard, 1982). Given the propensity of Odonata to inhabit microhabitats with warmer thermal regimes, a greater understanding of microhabitat occupancy and the variation in thermal regimes within water bodies is vital if we are to predict impacts of atmospheric warming. Adults of *Lestes sponsa* have been shown to exhibit body temperatures significantly higher than ambient temperature by perching in sunflecks (Watanabe and Taguchi, 1993). These sylvan damselflies were also able to utilise forced convection, the importance of which has been demonstrated experimentally in *Anax junius* (May, 1976), to reduce heat gain in sunflecks that were too warm. Anisoptera inhabiting deserts have been shown to exhibit substantially higher thoracic temperatures and thresholds for flight than congeners and conspecifics from cooler habitats, suggesting that a degree of adaptation to extreme thermal environments may be possible (Polcyn, 1994).

### 2.4.4. Activity patterns

As well as varying spatial patterns of activity, the temperate zone provides a broad thermal niche which can be exploited by varying temporal activity patterns. Corbet (1999) defines six discrete diel patterns of activity (DPA, see Figure 2.1) which rank along a continuum of thermal requirements from unimodal (UN – characteristic of odonates in temperate environments) to bimodal with activity only at sunrise and sunset (BRS – characteristic of some odonates in tropical environments). It might be expected that species would vary activity patterns across their ranges and, as the environment warms, over time at a single site.

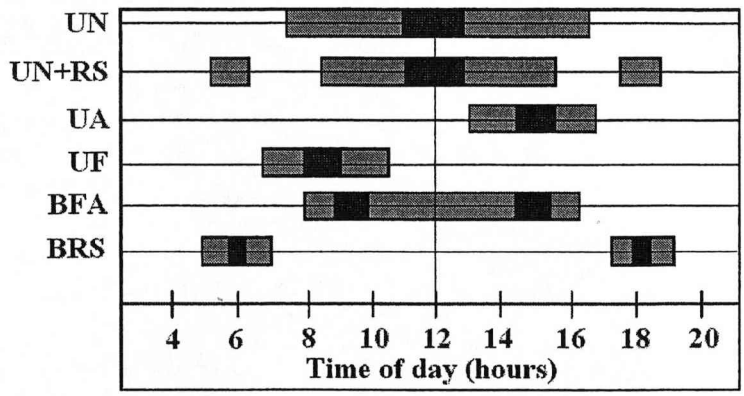


**Figure 2.1 – Proposed diel patterns of activity in Odonata (redrawn from Corbet, 2004). Grey bars indicate active periods and black regions are peaks in activity. UN: unimodal noon; UN+RS: unimodal noon plus sunrise and sunset; UA: unimodal afternoon; UF: unimodal forenoon; BFA: bimodal forenoon and afternoon; BRS: bimodal sunrise and sunset.**

### 2.4.5. Wing-whirring

In addition to the above mechanisms for thermoregulation, odonates also exhibit thermoregulatory behaviours more commonly seen in endotherms. In particular, a number of species perform 'wing-whirring', which enables a build up of metabolic heat originating in the flight muscles. At least one member of each American family of Anisoptera is capable of such behaviour and this can lead to warm-up rates of between 0.9 and 6.7°C·sec$^{-1}$ (May, 1976). Regulation of body temperature is also performed through controlling circulation of haemolymph through the thorax and abdomen (for a review of these topics, see May (1976)). However, some species are so adapted to their boreal habitat that they exhibit upper thermal thresholds for flight, e.g. *Aeshna caerulea* (Sternberg, 1997) and *Ischnura elegans* (Hilfert-Rüppell, 1998).

## 2.5. Ecology

### 2.5.1. Trophic interactions

Temperature has been implicated in determining the structure of aquatic communities (Heino, 2002, Carpenter et al., 1992, Burgmer et al., 2007). Latitudinal patterns in species richness have been documented for a number of taxa, including Odonata (Eversham and Cooper, 1998). As the climate warms, new communities will be formed as species shift their ranges at different rates (Hickling et al., 2006). Due to the sheer number of ecological interactions, it is impossible to consider all the implications of such community shifts. Mesocosm experiments have suggested that a 3°C increase in water temperature would have negligible impacts on the structure of aquatic

macroinvertebrate communities (Feuchtmayr et al., 2007), although natural odonate communities appear to exhibit high rates of turnover in response to changing climate (Flenner and Sahlén, 2008).

However, one change which may occur – with serious repercussions for the aquatic community – is the progressive extinction of fish populations (Xenopoulos and Lodge, 2006, Xenopoulos et al., 2005) coupled with the relatively low rate of colonisation in fish. While increases in the proportion of southerly distributed and warm water species have been reported in French rivers (Daufresne and Boët, 2007), islands such as the UK and Ireland can receive no such colonisation apart from by artificial means. The recognition of this problem has resulted in the resurrection of the concept of species introductions, rebranded as "assisted colonisation" (Hoegh-Guldberg et al., 2008).

In ecosystems in which they are present, fish dominate the rest of the food web by top-down pressure. However, fish also suppress large macroinvertebrate populations (Dorn, 2008) including Odonata (Bendell and McNicol, 1995, Henrickson, 1988, Feuchtmayr et al., 2007) and fish predation affects the size of macroinvertebrates (Blumenshine et al., 2000). As fish populations become extinct, there is the potential for odonates to assume the role of top predator. Certainly, any change in the dominant predator will have substantial (and potentially unpredictable) impacts on prey communities (Soluk, 1993). However, a brief comparison between the common fish *Gasterosteus aculeatus* (Actinopterygii) (Hynes, 1950) and detailed studies of *Ischnura elegans* (Thompson, 1978a) and *Cordulegaster boltonii* (Woodward and Hildrew, 2001) reveals a range of similarities in size and diet. The difference between fish and odonate predation certainly merits further research. Predation by fish on odonate larvae has also been linked to plant recruitment via the predation by adult odonates on pollinating insects (Knight et al., 2005). This highlights not only the complexity of natural systems but also the importance of considering the landscape and its constituent biotopes holistically.

The effects of varying temperature on the functional response of odonate larvae have been studied extensively in a number of species (Thompson, 1978c, Gresens et al., 1982). Higher temperatures result in an increase in the asymptotes of the type II functional response in *Ischnura elegans*. This was manifested in an increase in the attack coefficient and a decrease in handling time at higher temperatures (Thompson, 1978c). The increased feeding rates at higher temperatures have also been linked to an increase in the rate of gut clearance at higher temperatures (Gresens et al., 1982). Clearly an increase in feeding rate in a top predator in aquatic ecosystems (e.g. *Cordulegaster boltonii*; Woodward and Hildrew, 2001) will have knock-on effects at other trophic levels.

Attempts to model the population dynamics of *Ischnura elegans* (Crowley et al., 1987) have assumed a homogeneous prey population whose growth rate is related to temperature. However, the diversity of prey species available to a generalist such as an odonate and, therefore, the diversity of thermal responses are noted. As mentioned above, a further complication may arise through phenological decoupling of trophic interactions (Winder and Schindler, 2004). Trophic cascades resulting from such events could influence higher trophic levels including the Odonata.

### 2.5.2. Body size

Body size is potentially the most important parameter when considering an organism's ecology. It is also tightly linked to temperature, with larger body sizes at lower temperatures being reported in the majority of studies (for a review see Atkinson, 1994). Body size in Odonata has been showed to affect to diet breadth (Thompson, 1978b), handling time (Thompson, 1978c) and rate of consumption (Woodward and Hildrew, 2002). However, patterns in odonate body size have been under-studied.

The only attempt to quantify latitudinal variation in body size in Odonata was carried out by Johansson (2003). This study suggested a U-shaped relationship across the full extent of the geographical range, which has been tentatively explained using Bergmann and counter-Bergmann clines (Blanckenhorn and Demont, 2004). There is evidence that such a U-shape may have a genetic basis (De Block et al., 2008b).

### 2.5.3. Immunology

The effects of climate on invertebrate immunology have received relatively little attention, despite odonates having been studied extensively in the field and in the lab (Siva-Jothy, 2000, Siva-Jothy, 1999, Rantala et al., 2000, Robb and Forbes, 2005, Rolff, 2001, Robb and Forbes, 2006, Yourth et al., 2002). Only one study has considered the impact of temperature on odonate immunity, in the context of variation in immune function across the flight season (Robb and Forbes, 2005). This study clearly showed increased resistance to *Arrenurus planus* (Arachnidae: Arrenuridae) at higher temperatures, which results from higher haemocyte counts at higher temperatures (Pandey et al., 2007).

This temperature-mediated immunity may have implications for the determination of range margins. At a certain threshold of immune function, the immune challenge presented by the

pathogen community may be result in too great a mortality. This would lead to the kind of small, unstable marginal populations that are found in nature (Brown, 1984).

### 2.5.4. Distributions

A great deal of work has been carried out to detect changes in the distributions of flora and fauna in response to climate change (Hickling et al., 2006, Hitch and Leberg, 2007, Parmesan et al., 1999). However, before considering the implications of shifts in response to the current phase of warming, a historical context needs to be sought for these trends. This is provided by the literature on Quaternary climate change and associated shifts in distribution.

Quaternary climatic changes have been shown to be sudden and unpredictable (Adams et al., 1999). However, despite this insect populations appear to have survived with relatively little extinction (Coope, 1995b). It has been suggested that the morphological stasis exhibited by the insect fossil record through the quaternary is indicative of a high degree of dispersal which compensated for shifting fundamental niches (Coope, 1978). As mentioned above, the fact that extant taxa such as the Odonata possess a progenitor that has survived such rapid climatic transitions suggests that it has inherited a mechanism for surviving such challenges should they present themselves again (Balmford, 1996). However, contemporary rates of climate change are substantially greater than previously experienced and anthropogenic disturbance constitutes an entirely novel extinction threat.

Understanding how odonate ranges have responded to changing climate and predicting how these responses will be manifest in the future requires knowledge of the mechanisms that determine the realised niche. Although temperature has been supported as a potential factor, there are other candidates which may at least contribute and the traits on which temperature acts are not clear. An alternative climatic range determinant may be weather. Weather, and specifically the pattern of suitable oviposition days (Thompson, 1990), has been implicated in affecting fecundity of populations. Precipitation and cloud cover patterns follow approximately the same geographical distribution as isotherms, with higher cloud cover and precipitation at higher latitudes where temperatures are lower. Thus multiple climatic variables may work synergistically to restrict odonate populations at range margins.

Low temperature may also increase stress during development (Chang et al., 2007). Zygopteran wings have been shown to be uniform in shape along a latitudinal gradient until close to the range margin where populations exhibit wings that become progressively further from the 'normal' shape

(Hassall et al., 2008). It may be that this deviation from the norm is also a deviation from the most effective wing shape, leading to a decline in the fitness of populations exhibiting such deviations. Contemporary shifts in the distributions of Odonata have been reported where good historical data have been available (Hickling et al., 2006, Flenner and Sahlén, 2008, Ott, 1996, Aoki, 1997, Ott, 2007, Ott, 2001). Hickling et al. (2005) demonstrated a mean poleward shift in distributions of 74 km over 36 years between 1960 and 1995, or an annual shift of 2.1 km. This approximately corresponds to the upper limits of dispersal ability in extensively studied Zygoptera (Watts et al., 2004, Angelibert and Giani, 2003, Conrad et al., 1999) and to the rates of range expansion predicted from temperature models of *Gomphus vulgatissimus* (Braune et al., 2008). A substantially higher rate of expansion has been recorded in Swedish species (Flenner and Sahlén, 2008).

These results suggest that, given the appropriate habitat into which they may disperse, even the weaker-flying odonates, e.g. *Coenagrion mercuriale*, are capable of tracking changes in climate space. However, such a permeable habitat patch network is not guaranteed. Some regions contain high densities of lentic water bodies (Boothby and Hull, 1997), but future predictions suggest that the characteristics and distribution of water bodies may vary with changing climate (Dawson et al., 2003, Hostetler and Small, 1999, Carpenter et al., 1992). Climate-induced changes have also been predicted for lotic water systems (Pilgrim et al., 1998, Alcamo et al., 2003, Zwolsman and van Bokhoven, 2007) and some studies have attempted to predict how these changes might affect stream communities (Xenopoulos and Lodge, 2006).

## 2.6. Habitat

### 2.6.1. Drought

Some studies have investigated tolerance to drought in macroinvertebrates, including odonates. Studies examining recolonisation following drought events have shown that aquatic macroinvertebrates can rapidly return to former habitats following refilling (Van De Meutter et al., 2006). The removal of fish and subsequent lag in recolonisation relative to macroinvertebrates was suggested as a reason for the increase in diversity following refilling (Dorn, 2008, Van De Meutter et al., 2006). As mentioned above, fish are a major predator of Odonata and this may contribute to an expansion of odonate ranges. It should be noted, however, that some fish species also possess adaptations to drought, e.g. *Carassius carassius* (Actinopterygii) (Piironen and Holopainen, 1986).

The transition from permanent to temporary (both intermittent and episodic) water bodies that is predicted to occur in some cases (Carpenter et al., 1992) will affect different species in different

ways. The selective pressures that temporary water bodies exert on fauna are quite different to those in permanent water bodies (Williams, 1997). Some odonates possess adaptations that permit survival in seasonal ponds such as drought-resistant eggs, e.g. *Lestes* spp. (De Block et al., 2008a), drought resistant larvae, e.g. *Coenagrion hastulatum* (Valtonen, 1986), and rapid larval development, e.g. *Lestes sponsa* (Pickup and Thompson, 1990). *Ischnura pumilio*, an endangered species in the UK, also exhibits a drought-resistant egg (Cham, 1992) and this may aid in a recovery for the species if competitors are excluded by fluctuating water levels. Dragonfly assemblages inhabiting temporary wetlands in African desert and semi-desert areas differ from assemblages of non-desert areas and their constituent species tend to be highly mobile and multivoltine (Suhling et al., 2003).

Desiccation is a primary cause of egg mortality (Corbet, 2004) and so for species lacking such adaptations, reduced water permanence will reduce recruitment. This constitutes a substantial selective pressure towards the evolution of life-history traits that promote survival in more ephemeral water bodies, as has been seen in *Lestes* spp. (De Block et al., 2008a) and some species of Namibian Libellulidae (Suhling et al., 2005).

### 2.6.2. Pollution

Increases in temperature bring increases in evaporation from water bodies with concomitant increases in the concentrations of pollutants (Carpenter et al., 1992). Odonates have been shown to be sensitive to pollutants (Clark and Samways, 1996) and may suffer more than other taxa. Potential shifts in the trophic state of ponds and lakes due to warming (see Mooij et al., 2005 for a review) may also affect odonate persistence (Menetrey et al., 2005) as well as the macrophytes on which they rely for refuges (Thompson, 1987).

### 2.6.3. Landscape connectivity

A reduction in the number of habitable ponds will lead to a decline in the connectivity of the landscape. A range of modelling studies has attempted to calculate the impact of varying degrees of patch loss on landscape permeability (Collingham and Huntley, 2000, Opdam and Wascher, 2004, Travis, 2003). However, in order to assess the impact of habitat fragmentation on odonates, two factors must be considered.

Firstly, the habitat must be carefully defined. Many species exhibit idiosyncratic requirements of their environment which can render even the densest freshwater landscape unsuitable. *Sympetrum danae* epitomises this problem. A study of 1,000 ponds in the north of England showed that

*Sphagnum* species occurred in only 52 of the ponds (Boothby, 2000). The close association of *S. danae* with *Sphagnum* (Michiels and Dhondt, 1990) is likely what resulted in the species only being found in nine out of 1,000 ponds, despite being widespread in Britain (Merritt et al., 1996).

Secondly, dispersal ability needs to be quantified. Although a range of such studies exist (Hunger and Röske, 2001, Watts et al., 2004, Purse et al., 2003), these are ultimately limited by resources in the results that they can produce (Slatkin, 1985). Indeed, there appears to be a correlation between the size of the area surveyed in these studies on odonates and the amount of dispersal recorded (Figure 2.2), like that found for butterfly dispersal studies (Schneider, 2003).

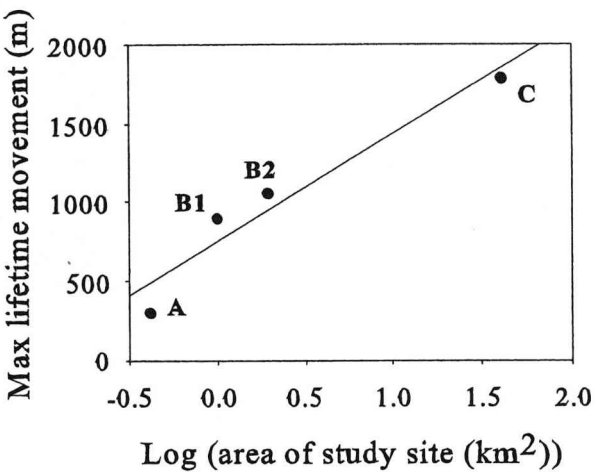


**Figure 2.2 – Relationship between the area of a study site and the maximum dispersal distance detected in four studies of *Coenagrion mercuriale* (r=0.966, p=0.034). A=Hunger & Röske (2001), B1=Purse et al. (2003) New Forest site, B2=Purse et al. (2003) Preseli site, C=Rouquette & Thompson (2007).**

In an extreme case of low landscape connectivity, insular populations of *Ischnura hastata* found on the Azores now exhibit uniform parthenogenesis (Cordero Rivera et al., 2005). It is possible that there are also parthenogenetic populations of other species on other islands (Sherratt and Beatty, 2005).

### 2.6.4. Sea-level rise

Another factor affecting habitat availability for Odonata may be predicted rises in sea levels (Meehl et al., 2005) and increasing frequency and severity of flood-causing precipitation events (Dale, 2005)

that accompany global warming. This pattern is predicted to lead to the loss of up to 22% of coastal wetlands globally by 2080 (Nicholls et al., 1999), although the extent may be greatly influenced by anthropogenic factors (Nicholls, 2004). The flooding that threatens much of the coastline of south east England (Shennan, 1993) has caused the extinction of *Coenagrion scitulum* in the UK (Hammond, 1997) and threatens the fenlands that represent a stronghold for many species including the endangered *Aeshna isosceles*. However, there has been little work done on the regional threats of inland freshwaters to sea-level rise. Although there are some odonates which are tolerant of brackish water (e.g. *Lestes dryas*), inundation of sites could lead to destruction of invertebrate communities and associated plant communities.

## 2.7. Evolution

### 2.7.1. Adaptation

The Odonata have a long evolutionary history over which relatively little phenotypic change has occurred. However, adaptations which likely have a thermal basis have occurred in a range of species. *Aeshna caerulea* is a boreal species which has developed both unusual basking behaviour and physiological colour change to cope with the severe climate (Sternberg, 1997). *Lestes* spp., on the other hand, have developed increased growth rates and drought-tolerant eggs to take advantage of ephemeral water bodies (De Block et al., 2008a). However, no within-species adaptation towards earlier egg hatching was found between populations of *L. viridis* inhabiting permanent and temporary water bodies (De Block et al., 2005).

On the other hand, within-species regional variations in growth rate (Leggott and Pritchard, 1985, Pritchard, 1989) and responses to seasonal cues for development (Norling, 1984c) have been demonstrated. The selective basis and costs of adaptive developmental rates are clearly laid out by Arendt (1997). This may be a profitable avenue for research given the observed shifts in critical photoperiod in *Aquarius paludum* (Harada et al., 2005). However, no unequivocal adaptation during the current phase of climate warming has been documented.

### 2.7.2. Processes at range margins

As climate space expands, it is intuitive to suppose that new habitats will be colonised by a non-representative sample of genotypes from the potential source populations. It has been proposed that populations at "marginal" sites may possess exaggerated dispersal traits compared to those in "core" sites because of the propensity for more highly dispersing individuals to found populations at the expanding range margin (Simberloff, 1981). Examples include an increase in the proportion of

macropterous (dispersing) individuals of four species of bush crickets in marginal populations relative to core populations (Simmons and Thomas, 2004), increased flight muscle relative to body mass in recently founded populations of *Pararge aegeria* (Lepidoptera: Nympalidae) (Hill et al., 1999a) and the progressive increase in leg length during invasion of Australia by *Bufo marinus* (Amphibia) (Phillips et al., 2006).

In the case of Odonata, such dispersal traits may include proportionally larger thoraces (i.e. greater flight muscle mass), lower wing loading, higher wing aspect ratio and increased body size. Some of these traits (e.g. wing loading) have been studied in Odonata but analyses have focused on interspecific variation rather than intraspecific variation (Grabow and Rüppell, 1995). In addition to increases in the magnitude of dispersal traits, there may be a concurrent decrease in the magnitude of non-dispersal traits reflecting a trade-off based on finite energy resources. Such a trade-off may involve declines in fecundity (e.g. a reduction in abdominal mass leading to a reduction in wing loading) or a decline in immune function.

## 2.8. Extinction risk

Although a warm-adapted taxon, local populations of temperate Odonata are certainly at risk from the rate and extent of projected climate change. This risk results from the loss of fundamental niche space due to geographic constriction at northern range margins. Such a pattern is seen in southern populations of *Leucorrhinia dubia*, which are restricted to isolated, high altitude sites in the Pyrenees and Alps (Askew, 2004). Fortunately most species, including *L. dubia*, have access to northern habitats into which the range can shift – particularly northern Scandinavia and Russia, which will likely see a large increase in species numbers over the coming years.

A further problem with climate change is the indirect effect of temperature on sea level. Many of the most diverse odonate communities persist in low-lying wetlands such as the Fens in England and the wetlands of the Netherlands, which are below sea level. Inundation by sea water of vast areas appears to be almost inevitable given the present rate of sea level rise (Meehl et al., 2005). As mentioned above, flooding has already been implicated in the extinction of *Coenagrion scitulum* from southern England.

One hundred odonate species are listed on the IUCN red list as being either endangered or critically endangered (for a review of IUCN regional reports, see International Journal of Odonatology, vol. 7, issue 2). Only two species are thought to be extinct, both of which are insular: *Megalagrion jugorum*

from the Hawaiian Islands and *Sympetrum dilatatum* from the Atlantic island of St Helena (IUCN, 2008). This observation and their extensive evolutionary history suggest that Odonata are robust to extinction pressures. However, it must be borne in mind that insect extinctions are difficult to verify (Dunn, 2005), even in relatively conspicuous species such as Odonata.

## 2.9. Summary

The Odonata exhibit a range of adaptations that allow them to respond to variations in temperature. This enables them to persist in fluctuating environments, sometimes spanning a broad range of abiotic conditions. The responses exhibited by Odonata to varying thermal regimes have been detected at a range of scales from the physiological studies of May (1976) through the behavioural experiments of Thompson (1978c) to the macroecological observations of Hickling et al. (2006) and Hassall et al. (2007).

It is likely that future impacts on odonates will largely involve a spatial shift of communities and their associated ecological interactions. However, this relies on the rates of responses of trophic, dispersal and developmental traits being equal among species, a situation which is highly unlikely. The majority of species are predicted to benefit from the warming through poleward expansions of range. Even in boreal species, climate space often still exists beyond the current geographical distribution. However, a particular threat to odonates comes in the form of habitat fragmentation. Species-specific habitat requirements, pollution and mismanagement of water bodies result in what appears to be a dense network of water bodies being largely unusable for some species. This, coupled with poor dispersal, represents a challenge to the tracking of climate space by certain species.

Much more research is required into the Odonata, not only because they represent an important part of many aquatic communities but also because this taxon's thermal sensitivity makes it a potential barometer for environmental change. Such research should focus on the physiological responses underlying broad-scale patterns of change. Specifically: the identification of range-determining factors through physiological experiments and experiments to investigate the difference in systems with and without vertebrate predators.

# *Chapter 3. Historical changes in the phenology of British Odonata are related to climate*

## 3.1. Abstract

Responses of biota to climate change take a number of forms including distributional shifts, behavioural changes and life history changes. This study examined an extensive set of biological records to investigate changes in the timing of life history transitions (specifically emergence) in British Odonata between 1960 and 2004. The results show that there has been a significant, consistent advance in phenology in the taxon as a whole over the period of warming that is mediated by life history traits. British odonates without an egg diapause significantly advanced the leading edge (first quartile date) of the flight period by a mean of 2.73 ± 0.055 days per decade (S.E., $n$=17) or 5.82 ± 1.15 (S.E., $n$=17) days per degree rise in temperature. The results suggest that the damped temperature oscillations experienced by aquatic organisms compared to terrestrial organisms are sufficient to evoke phenological responses similar to those of purely terrestrial taxa.

## 3.2. Introduction

A trend in environmental warming is now undeniable (Karl and Trenberth, 2003). Whether anthropogenic or natural, the effects on a wide range of global flora and fauna are significant and startling (Hughes, 2000, Parmesan and Yohe, 2003, Root et al., 2003). Physiological limits for temperature tolerance place restrictions on the persistence of organisms in the face of consistent changing temperature.

Coope (1995b) has highlighted three potential responses to persistent climate change: (i) the species can become extinct, (ii) the species can adapt *in situ*, and (iii) the species can migrate to areas with a more tolerable climate. There are examples of species that may have succumbed to the pressures of contemporary climate change (e.g. Pounds et al., 2006). Evolution appears to play a very minor role in faunal responses to climate change (Coope, 1978), although selection may have a more significant effect in plants (Davis et al., 2005). Large-scale distributional changes have been recorded numerous times (Hickling et al., 2006, Parmesan et al., 1999, Mieszkowska et al., 2006). However, flexibility inherent in an organism's life cycle may buffer against the impacts of climate change, thus altering the threshold at which the organism must resort to one of those responses.

Complex life histories have evolved in insects which enable them to cope with seasonal fluctuations in climate, permitting maximum exploitation of warmer seasons while cooler seasons are survived

by more resistant forms (Butterfield and Coulson, 1997). The mechanism for seasonal regulation most commonly involves the use of cues such as environmental temperature and photoperiod to determine when to undergo life history transitions (Lutz, 1974). The issue of photoperiod has received attention in a variety of taxa (Vaz Nunes and Saunders, 1999). Critical photoperiods (the day lengths that result in the commencement of diapause) have been shown to vary latitudinally within the same species (Norling, 1984c) and there is evidence that critical photoperiods are changing with time as environmental warming increases amenable growth season (Harada et al., 2005).

Photoperiod also acts at the end of the flight season to create a "time stress", resulting in accelerated development in individuals exposed to photoperiods characteristic of later in the season (Norling, 1984b, Johansson and Rowe, 1999). This increase in developmental rate serves to restrict the trailing edge of the flight period. However, because of the reliance of this effect on photoperiods, it is unlikely that environmental warming will affect the latter part of the odonate flight period.

The Odonata are an ancient order, with all active stages of the life cycle being voracious carnivores. Distributional responses of some Odonata to environmental warming have been noted in some anecdotal studies (Aoki, 1997, Ott, 1996) and recently Hickling et al. (2005) produced a far more conclusive review of the British species. This study showed that there was a trend towards a northward shift in those range margins that occurred in Britain. With changes in mean environmental temperature over the past century, it seems reasonable to suppose that there will also be concurrent changes in the timing of life history transitions. Such changes in phenology have been documented using biological records in a variety of British animals, including Lepidoptera (Sparks and Yates, 1997, Roy and Sparks, 2000), Homoptera (Fleming and Tatchell, 1995) and birds (Crick et al., 1997), as well as flowering plants (Sparks et al., 2000).

The long-term phenological response of Odonata to changing environmental temperature has not been investigated. This study seeks to examine an extensive collection of biological records in an attempt to discern patterns in flight period for British Odonata over the recent period of warming. Part of the flexibility in the odonate life cycle that permits variation in emergence phenology is due to periods of diapause which, depending upon species, can exist in the egg (Ando, 1962) or the larva (e.g. Corbet et al., 1989) with hibernation (e.g. *Sympetrum striolatum*; Jödicke and Thomas, 1993) or aestivation (e.g. *S. striolatum*; Parr, in Pritchard, 1992) in the adult. Periods of diapause either occur

over autumn/winter in temperate-centred species or, in the case of aestivation, through summer dry periods in tropical species.

Temperature can influence a variety of aspects of odonate biology. In the egg stage, both diapause development (Sawchyn and Church, 1973) and hatching (Sawchyn and Gillott, 1974b, Sawchyn and Gillott, 1974a) are temperature dependent. In the larval stage, feeding rates (Thompson, 1978c), development time (Pritchard, 1989) and larval ecdysis (Lutz, 1974, Corbet, 1957) are controlled by temperature. In the adult stage, flight periods (Hilfert-Rüppell, 1998) and colour-change (Sternberg, 1996) are affected by temperature. Of the effects mentioned above, egg hatching, larval ecdysis and larval development time are most relevant to phenology.

Were environmental temperatures to increase, it would be expected that egg hatching dates would occur earlier in the year. In "summer species" (Corbet, 1954) where lower temperature thresholds (LTTs) for ecdysis occur (Corbet, 1957), these would be reached earlier in the year under conditions of environmental warming leading to advances in phenology. Similar advances in phenology would be expected for species that overwinter in the final instar ("spring species" (Corbet, 1954)) due to threshold temperatures (which, along with long photoperiods, constitute permissive conditions for metamorphosis (Corbet, 1999)) occurring earlier. Impacts on larval development times are more complex in temperate regions due to the presence of semi- and partivoltine species. Norling's (1984b) model of photoperiodic responses in seasonal regulation posits a "winter critical size" (WCS) which, if exceeded by larvae in the winter, causes a reversal of the long photoperiod induced diapause during the next summer. This results in accelerated development during long photoperiods and emergence that year. If temperatures increase, it is logical to suggest that larval development times will decrease and increasing proportions of individuals within a population will reach the WCS, leading to changes in voltinism. Such voltinism changes would alter peaks in emergence according to the varying proportions exhibiting different development times.

Some British species of Odonata exhibit a diapause in the egg stage which can take one of two forms: type 1 egg diapause where katatrepsis (the rotation of the embryo inside the egg) occurs after winter or type 2 egg diapause where katatrepsis occurs before winter (Ando, 1962). The egg diapause alters the exposure of the larvae to the low winter temperatures and prior exposure to low temperatures has been shown to affect photoperiodic responses in larvae (Corbet et al., 1989, Ingram, 1975), so it may be that species exhibiting an egg diapause respond differently to changing spring temperatures than those that do not exhibit such a diapause. Advances in emergence dates

may be expected to result from (i) threshold temperatures for metamorphosis occurring earlier for spring species, (ii) LTTs for ecdysis being reached earlier for summer species and (iii) variation in larval exposure to low temperatures between species that possess and lack an egg diapause.

Previous studies have shown patterns between purely terrestrial insect taxa and changes in ambient temperature (Sparks and Yates, 1997, Fleming and Tatchell, 1995). By contrast, this study investigates the impact of changing environmental temperature on the phenology of a taxon that has a sensitive period during an aquatic life history stage and occupies a range of thermally varying habitats. Such work on phenology has come to the fore since changes in phenology were included in the UK government's indicators of climate change (Cannell et al., 1999).

## 3.3. Methods

### 3.3.1. The British Dragonfly Society database

The British Dragonfly Society (BDS) maintains a database of sightings of Odonata from between 1807 and the present. At the time that the database was analysed (28th November 2005), it contained 448,547 records. These records included sightings of individuals (as larvae, adults and exuviae), as well as separate records for selected behaviours (emerging, copulating and ovipositing). However, only records of sightings of adults in Britain between 1960 and 2004 were included, since this period represents an anomalous period of warming (Jones and Mann, 2004) and increased recorder effort. Records were also excluded if they were deemed to be duplicates or if they did not have a precise date. This reduced the number of records to 268,772. Only records recorded between the latitudes of 50 and 52°N were included to restrict latitudinal variation in flight periods, leaving 217,896 records for the analysis. This latitudinal band represented the greatest concentration of records, with higher latitudes having too few to produce reliable results.

Only established, non-migratory British species were selected. According to the BDS species list (http://www.dragonflysoc.org.uk), *Aeshna mixta*, although formerly migratory, is now considered a British species. More recently *Erythromma viridulum* has been added to the list, but would be of no use in this study due to its relatively short history in the database. The *Sympetrum* spp. that migrate into Britain in waves before becoming extinct (*S. fonscolombii* and *S. flaveolum*) are classified as "migrant/vagrant" and were excluded from the analysis. *S. nigrescens* was excluded on the basis that it most likely constitutes a melanic form of *S. striolatum* (Merritt and Vick, 1983). This selection process left 37 species.

The annual mean of the Central England Temperature (CET) index was used as a general indicator of British temperatures and was obtained from the Met Office's Hadley Centre. CET has been found to correlate with other regional temperatures and has been used in previous analyses of phenology (Sparks and Carey, 1995, Sparks and Yates, 1997). The annual mean CET between 1960 and 2004 was significantly correlated with spring (March, April and May; $r$=0.693, $p$<0.001), summer (June, July and August; $r$=0.701, $p$<0.001) and winter (December, January and February; $r$=0.731, $p$<0.001) mean temperatures and so was used as an indicator of general temperature change over the period.

### 3.3.2. Analysis

For each species the records were divided into time periods. This was done in a species-specific way to maximise the resolution in each case. The longest time period was a decade, with the rarest species being grouped into 1960-1969, 1970-1979, 1980-1989, 1990-1999 and 2000-2004 when there were between 30 and 499 records in each period. Periods with fewer than 30 records were excluded. Where there were between 500 and 999 records in a decade, those records were divided into two groups for the first and second half of that decade. Where there were between 1,000 and 4999 records in a decade, those records were divided into 3-year blocks (e.g. 1980-2, 1983-5, 1986-8 etc). In some cases decades exceeded 5,000 records and these were divided into 2-year blocks (e.g. 1980-1, 1982-3, 1984-5 etc). A conservative rule was required because records were not evenly distributed over the years and so care had to be taken to ensure that sufficient records were present in each period.

Species were excluded if they could not be split into 5 or more time periods to maintain the accuracy of the estimated slopes. This led to the omission of *Aeshna caerulea*, *Aeshna isosceles*, *Brachytron pratense*, *Coenagrion hastulatum*, *C. mercuriale*, *C. pulchellum*, *Gomphus vulgatissimus*, *Ischnura pumilio*, *Lestes dryas*, *Leucorrhinia dubia*, *Libellula fulva* and *Somatochlora arctica*.

The date of each record was then converted into a Julian date. The first quartile (Q1), median (Q2) and third quartile (Q3) were calculated from the distribution of Julian dates for each time period. Due to small sample sizes (5-11 points) non-parametric regression techniques were used. Kendall's robust line-fit method (Sokal and Rohlf, 1995) produced estimates of the slope of the line describing the relationship between date and temperature and each of the 3 flight date statistics. In addition, the relationships between the flight dates and the residuals of the regression of temperature on year were found in order to assess the impact of temperature anomalies on phenology. However, in averaging temperatures over a number of years in an attempt to maximise the accuracy of the flight date statistics, it is likely that the temperature anomalies will have been smoothed-over. To test

this, *Pyrrhosoma nymphula* (a highly recorded species) was analysed using records for individual years.

A p-value for each of the lines was obtained using Kendall's rank correlation. A Bonferroni correction was employed to correct for the number of tests (144) and this reduced the α-level to 0.00035. Samples of slopes for each date-factor combination were analysed using 2-tailed, 1-sample *t*-tests with test means of zero. Samples of slopes for Q1 flight dates were further analysed with 1-tailed, 1-sample *t*-tests to test the hypothesis that these dates were advancing.

Felsenstein (1985) first highlighted the fact that phylogeny had to be taken into account when comparing species. However, "all comparisons should start with a reliable phylogeny" (Stearns and Hoekstra, 2005, p.349) and although much effort has been expended in attempting to elucidate both higher (Rehn, 2003, Carle, 1982, Bechly, 1996, Trueman, 1996) and deeper (May, 2002, O'Grady and May, 2003, von Ellenrieder, 2002, Artiss et al., 2001) relationships within odonate phylogeny, a complete phylogeny for the British species is still lacking. In the absence of such a phylogeny, evolutionary relationships were partially controlled for by averaging across slopes from congeners in the analysis of samples of slopes (leaving 16 data).

In investigating factors affecting phenological response, phylogeny was controlled for using a GLM with type I (sequential) sum of squares with "family" as the first term in the model (Hof et al., 2006). All nine sets of slopes were checked for normality (Anderson-Darling test) and homoscedasticity before analysis. Factors analysed included presence/absence of egg diapause (Merritt et al., 1996, using information in Corbet, 1999). Species defined as having an egg diapause were further divided into those with obligate and those with facultative egg diapause. Also investigated was the classification as "spring" or "summer" species (according to Corbet et al., 1960). Corbet (1954) defined "spring" species as those which overwinter in late instars and emerge synchronously in the spring in response to temperature and photoperiodic cues. Summer species overwinter in earlier instars and undergo a number of moults before emerging asynchronously in the summer.

The distribution of records in the BDS database is temporally uneven. Statistics relating to the flight periods were tested for each species to assess the impact of increasing numbers of records at the latter end of the recording period. Since there were 3 correlations per species and 24 species, a Bonferroni adjustment was used to reduce the alpha level to that required for significance at 72 tests (new $\alpha$=0.00069).

**Table 3.1 – Slopes of relationships between annual temperature anomalies ("residuals" – the residuals of the regression of temperature on year), year and mean Central England Temperature ("mean CET") and three flight period statistics (first, second and third quartile flight dates). All figures are Kendall's τ. Although some relationships were significant at α=0.05, Bonferroni's correction resulted in all results being non-significant. * = species with an obligate egg diapauses, † = species with a facultative egg diapause,**

| | Residuals | | | Mean CET | | | Year | | |
|---|---|---|---|---|---|---|---|---|---|
| | Q1 | Q2 | Q3 | Q1 | Q2 | Q3 | Q1 | Q2 | Q3 |
| **Spring species** | | | | | | | | | |
| *Anax imperator* | 8.44 | 0 | -1.37 | -3.85 | 0 | -3.17 | -0.458 | -0.133 | -0.182 |
| *Calopteryx splendens* | -3.55 | 2.56 | 8.46 | -3.11 | 3.53 | 7.78 | -0.06 | 0.242 | 0.41 |
| *Calopteryx virgo* | -7.75 | 19.8 | 23.2 | 0.699 | 14.2 | 21.4 | 0.0397 | 0.397 | 0.67 |
| *Cordulegaster boltonii* | 5.64 | 4.92 | 7.38 | 3.96 | 4.46 | 8.49 | 0.0724 | 0.131 | 0.667 |
| *Cordulia aenea* | -8.7 | -10.4 | -17.5 | -1.95 | -7.59 | -16.9 | -0.0789 | -0.519 | -0.522 |
| *Erythromma najas* | 6.07 | 11.8 | 14 | -7.08 | -0.391 | 10.41 | -0.283 | -0.146 | 0.279 |
| *Libellula depressa* | -19.5 | -8.14 | -3.85 | -12.8 | -6.4 | -8.22 | -0.479 | -0.462 | -0.484 |
| *Libellula quadrimaculata* | -13.8 | -2.29 | 5.07 | -8.13 | -6.16 | -3.45 | -0.41 | -0.461 | -0.312 |
| *Orthetrum cancellatum* | 0 | 12 | 3.8 | -2 | 0 | 3.23 | -0.134 | -0.075 | 0.131 |
| *Orthetrum coerulescens* | 3.8 | -3.59 | 5.52 | -9.04 | -1.83 | 2.77 | -0.444 | -0.166 | 0.103 |
| *Platycnemis pennipes* | -3.09 | 3.09 | 11.7 | 0 | 2.06 | 12.36 | 0.0385 | 0.1 | 0.308 |
| *Pyrrhosoma nymphula* | -9.32 | 0 | -3.88 | -13.1 | -14.1 | -12.6 | -0.583 | -0.778 | -0.625 |
| *Somatochlora metallica*† | -22.6 | -40 | -12.4 | 1.59 | -1.08 | -1.35 | 0.226 | 0.509 | 0.113 |
| **Summer species** | | | | | | | | | |
| *Aeshna cyanea** | 5.61 | 10.3 | 5.04 | 2.83 | 1.82 | 0.57 | 0.127 | 0.0268 | 0.0233 |
| *Aeshna grandis** | 0 | -4.94 | -4.66 | -4.68 | -6.04 | -6.35 | -0.267 | -0.368 | -0.3333 |
| *Aeshna juncea** | 22.2 | 26.8 | 16.1 | 3.74 | 9.77 | 5.83 | 0.0192 | 0.535 | 0.46 |
| *Aeshna mixta** | -1.08 | 0 | -6.71 | -6.53 | -4.4 | -5.48 | -0.197 | -0.29 | -0.272 |
| *Ceriagrion tenellum* | -2.26 | -0.139 | 8.82 | -1.47 | 1.8 | 7.31 | -0.064 | -0.00081 | 0.158 |
| *Coenagrion puella* | -6.55 | 0 | 0 | -9.4 | -7.69 | 0 | -0.275 | -0.375 | 0.0543 |
| *Enallagma cyathigerum* | 4.36 | 3.7 | 3.7 | -2.38 | 1.96 | 1.81 | -0.359 | -0.0833 | 0 |
| *Ischnura elegans* | 0 | 3.71 | 0 | -4.53 | -3.37 | 0.974 | -0.333 | -0.214 | 0.0526 |
| *Lestes sponsa** | 2.9 | 2.9 | 8.62 | 2.22 | 3.33 | 4.96 | 0.1645 | 0.167 | 0.115 |
| *Sympetrum danae** | 14 | 27.1 | 16.6 | 3.49 | 9.19 | 1.39 | 0.136 | 0.351 | 0.119 |
| *Sympetrum sanguineum*† | -8.34 | -5.75 | -12.5 | 3.5 | 0.875 | 0 | 0.333 | 0.273 | 0.0909 |
| *Sympetrum striolatum*† | -2.07 | 2.14 | -0.535 | -0.81 | 2.04 | 4.41 | 0.0714 | 0.111 | 0.3 |

## 3.4. Results

### 3.4.1. Recorder effort

The number of records in the BDS database is biased temporally, with vastly more records in later periods. However, there were no significant correlations for any species between the number of records and Q1, Q2 or Q3 flight dates at the reduced alpha level.

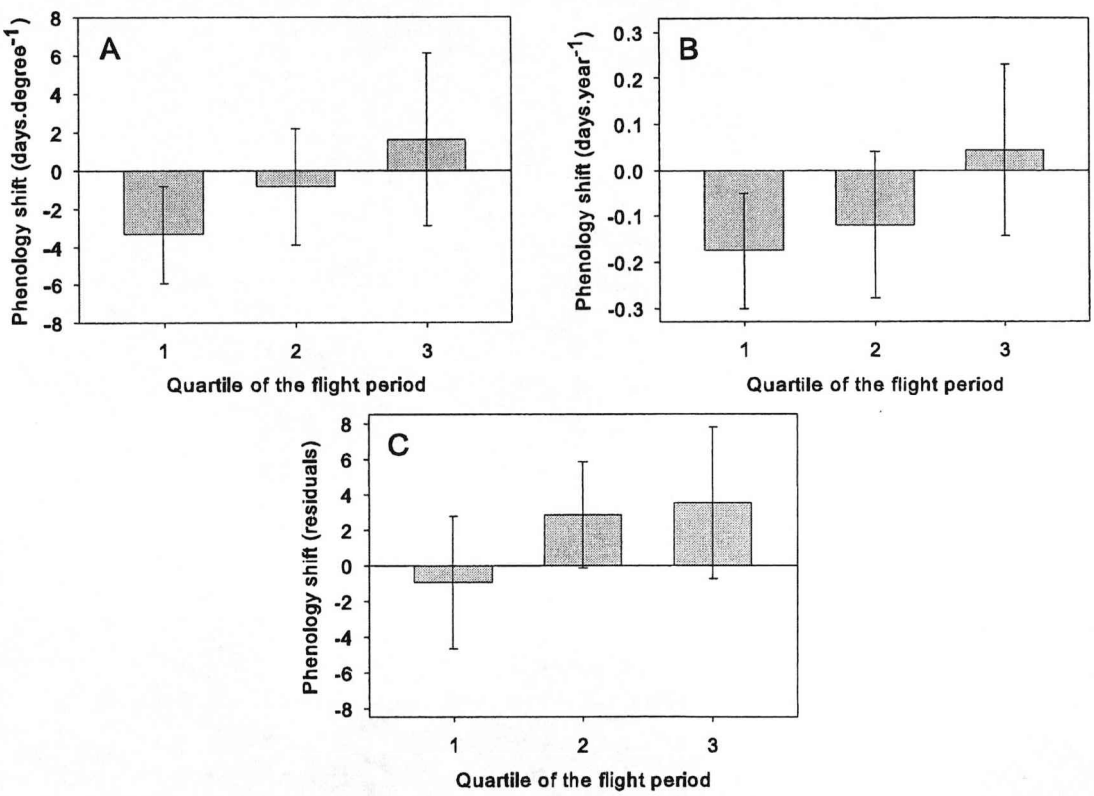


**Figure 3.1 – Rates of change in the phenology of Q1, Q2 and Q3 flight dates in relation to (A) changing temperature, (B) year and (C) temperature anomalies (residuals of temperature on year) between 1960 and 2004. Bars are 95% confidence intervals.**

### 3.4.2. Changes in phenology

There were no significant shifts in phenology that persisted after the reduction of the α-value resulting from the Bonferroni correction (see Table 3.1). Slopes (Kendall's τ values) for all species were pooled for each predictor-response combination (i.e. for each column of Table 3.1). The samples of slopes for the Q1 flight date against both mean CET and year were found to be

significantly different from zero in the 2-tailed *t*-tests (Q1 and mean CET, $t$=-2.69, $p$=0.013; Q1 and year, $t$=-2.55, $p$=0.018; Figure 3.1A and B), a result that persisted after controlling for phylogeny (Q1 and mean CET, $t$=-2.65, $p$=0.017; Q1 and year, $t$=-2.54, $p$=0.022). This pattern was also seen in the 1-tailed, 1-sample *t*-tests when phylogeny was controlled for (Q1 and mean CET, $t$=-2.81, $p$=0.009; Q1 and year, $t$=-3.00, $p$=0.011).

Neither median nor Q3 flight statistics advanced significantly in the taxon as a whole with temperature or date. There were also no significant relationships between flight dates and the residuals of the regression of temperature on date (Figure 3.1C). However, flight statistics for years in which more than 30 records had been taken (1978-2004) for *Pyrrhosoma nymphula* were highly significantly and negatively correlated with the residuals (Q1, $r$=-0.608, $p$=0.001; median, $r$=-0.629, $p$<0.001; Q3, $r$=-0.471, $p$=0.013), confirming the independent effect of temperature on the phenology of this species. Unfortunately, such large numbers of records were not available for other species.

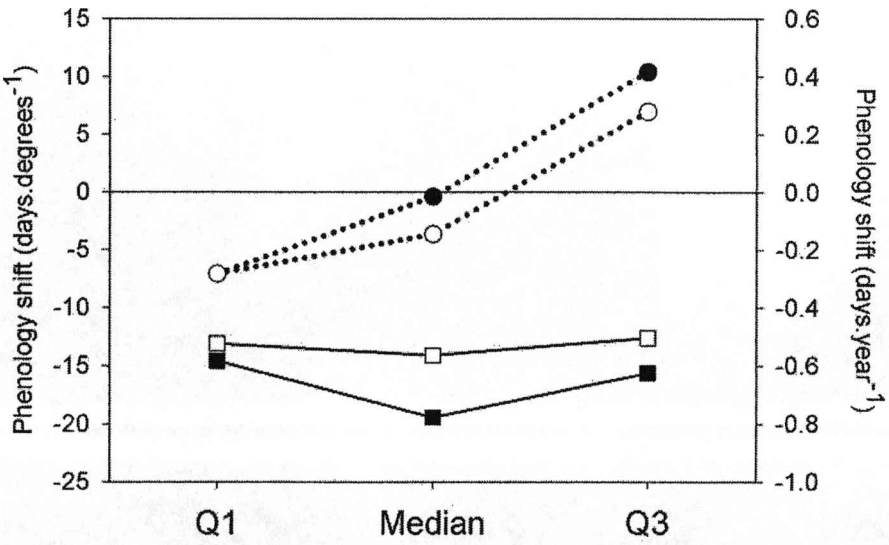


**Figure 3.2 – Shifts in the flight periods of *Pyrrhosoma nymphula* (squares) and *Erythromma najas* (circles). Open symbols indicate shifts in relation to year and closed symbols indicate shifts in relation to temperature.**

### 3.4.3. Traits affecting response

After controlling for phylogeny, spring and summer species were found to differ in the phenological responses at the Q1 flight date both in relation to year and temperature. Spring species tended to exhibit a greater advance in phenology than summer species. Species with an egg diapause (either obligate or facultative) tended to advance their phenology to a lesser extent than species without an egg diapause. This was a significant effect in Q1 and Q2 in relation to year and approached significance in relation to CET.

Phylogeny appeared to have a significant effect on the response of species to temperature anomalies. However, this could result from a single family, the Corduliidae (represented only by *Somatochlora metallica* and *Cordulia aenea*), giving anomalously extreme slopes. Only 5 data were available for *S. metallica* and 7 for *C. aenea*, so error margins were relatively high for this group.

**Table 3.2 – Results of GLM to control for phylogeny (see text for details).**

| | | Family | | Spring/summer | | Family | | Egg diapause | |
|---|---|---|---|---|---|---|---|---|---|
| | | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* |
| Residuals | Q1 | 1.90 | 0.139 | 0.67 | 0.423 | 1.99 | 0.127 | 1.24 | 0.316 |
| | Median | 2.27 | 0.086 | 0.43 | 0.522 | **3.13** | **0.032** | **4.01** | **0.039** |
| | Q3 | 2.49 | 0.065 | 0.14 | 0.711 | **2.95** | **0.039** | 2.14 | 0.150 |
| Mean CET | Q1 | 1.21 | 0.350 | **6.23** | **0.023** | 1.21 | 0.353 | 3.60 | 0.051 |
| | Median | 1.43 | 0.260 | 2.15 | 0.160 | 1.41 | 0.271 | 0.266 | 1.44 |
| | Q3 | 2.38 | 0.074 | 0.16 | 0.698 | 2.49 | 0.068 | 0.94 | 0.410 |
| Year | Q1 | 1.39 | 0.275 | **8.58** | **0.009** | 2.01 | 0.124 | **10.53** | **0.001** |
| | Median | 0.83 | 0.566 | 3.03 | 0.100 | 1.04 | 0.438 | **4.57** | **0.027** |
| | Q3 | 1.97 | 0.128 | 1.60 | 0.222 | 2.13 | 0.107 | 2.06 | 0.160 |

Significant results are highlighted in **bold** type. CET = Central England Temperature.

## 3.5. Discussion

As a taxon, British Odonata have significantly advanced their phenology chronologically (on average by 1.75 days per decade) and with respect to temperature (on average by 3.37 days per 1°C increase) over a 45 year period (1960-2004). This shift represents an extension to the preceding edge of the flight period (first quartile flight date) as opposed to a shift of the flight period as a

whole. This is the first phenology study of a taxon that is restricted to freshwater bodies to breed and concurs with the findings of studies on terrestrial British invertebrates (Sparks and Yates, 1997, Fleming and Tatchell, 1995, Roy and Sparks, 2000).

In addition to being biased temporally, the records most likely represent sightings of mature individuals, rather than the full population demographic. During the prereproductive period, odonates possess a negative taxis towards reflective surfaces, causing them to disperse varying distances from their natal water body (Corbet, 1999). This is reversed during maturation to cause an aggregation of adults at water bodies at the start of the reproductive period. Many of the adults sighted will have been more mature individuals at water bodies where adults are at their highest concentrations and, hence, most noticeable. This means that the leading edge of the flight period (as indicated by the Q1 flight date) will slightly underestimate the actual date at which the species emerges, an effect that will be constant throughout the records.

Another factor that may influence results is the varying size of water body in which the different species live. The size of the water body affects the buffering of ambient temperature fluctuations and, therefore, the perception of temperature by aquatic organisms. However, odonates are known to seek out warmer microclimates within water bodies, e.g. *Aeshna caerulea* (Sternberg, 1997), such as riparian vegetation, where such buffering is less effective. The data are not available to study this factor.

### 3.5.1. Phenology of the flight period

The absence of a shift in the Q3 flight date is harder to explain. Having concluded that most species are advancing in phenology, it would be sensible to predict that the end to the flight season should either (i) advance in a similar way or (ii) regress to mirror the advance of Q1 about the mean flight date.

In support of the former prediction, daily survivorship is constant throughout adult life in many species, e.g. *Coenagrion puella* (Banks and Thompson, 1985b), with some studies showing an increased mortality at the beginning of the reproductive period, e.g. *Enallagma hageni* (Fincke, 1982). Therefore, if all individuals share the same cue for seasonal regulation, they should all emerge, live and die at earlier points through the year according to a type II survivorship curve. This pattern appears to be exhibited by *Pyrrhosoma nymphula*, which shows similar advances in Q1, median and Q3 flight dates (Figure 3.2).

The latter hypothesis is based on the assumption that insects die or become less active in winter due to abiotic factors such as falling ambient temperatures. If global warming is alleviating the temperature stress at the end of the flight season then it seems reasonable to expect that there will be more individuals on the wing at a later date (especially in those species with asynchronous emergence periods). *Erythromma najas* seems to follow this pattern, with shifts of similar magnitude but in opposite directions in the Q1 and Q3 flight dates and little change in the median (Figure 3.2).

The fact that neither of these patterns is seen as a general pattern in the taxon as a whole suggests that either (i) neither hypothesis is correct and there are other factors governing the species-specific response of the latter part of the flight period, or (ii) that both factors are working antagonistically in odonates as a whole.

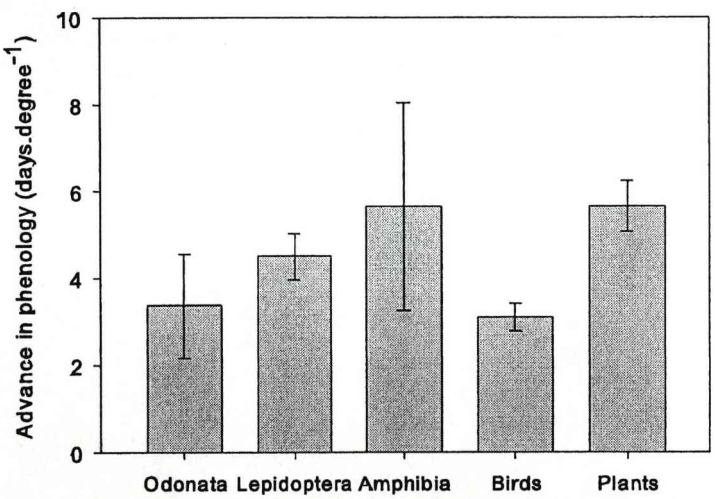


**Figure 3.3 – Comparison of shifts in phenology of Odonata with those of other taxa. Lepidoptera data are from Roy and Sparks (2000), Amphibia data are from Gibbs and Breisch (2001), bird data are from Crick and Sparks (1999), and plant data are from Sparks et al. (2000).**

### 3.5.2. Phenology and life-histories

As previously noted, Odonata possess a number of life history traits which allow regulation of the life cycle in response to environmental conditions. One such trait is the egg diapause, which involves eggs overwintering and hatching in response to increasing temperatures (Corbet, 1956b) (and

sometimes increasing water levels (Sawchyn and Gillott, 1974b)) in spring. In univoltine species the larvae then develop through the spring, emerging asynchronously in summer. In semi- or partivoltine species larval development continues through the year and the following winter is spent as a larva. Species which do not possess a diapause in the egg stage tend to overwinter as late-instar larvae and use warming temperatures and photoperiod in spring as a cue for metamorphosis (Corbet, 1999). The results of this study suggest that species without an egg diapause have flight periods which are more sensitive to increasing temperatures than species that do possess an egg diapause. This may be due to variations in exposure of larvae to low temperatures during winter.

The results also suggest that the variation in the use of rising vernal temperatures between spring and summer species results in a variation in response to environmental warming. The cause of this difference in response may stem from the fact that winter and spring temperatures are increasing faster than summer and autumn temperatures (Bonsal et al., 2001). Thus, spring species, which use only spring temperatures as a seasonal cue, would be more affected than summer species which use a combination of spring and summer temperatures during their progression through LTTs.

## 3.6. Conclusions

The Odonata are a warm-adapted taxon (Pritchard and Leggott, 1987) which may favour their chances of surviving climate change. This group has been shown to shift ranges poleward (Hickling et al., 2005) (although this ability may be affected by changing distributions of freshwaters (Dawson et al., 2003)), respond morphologically to variations in habitat configuration (Taylor and Merriam, 1995), adapt to external cues for seasonal regulation (Norling, 1984c) and, in the present study, take advantage of climatic warming to expand their flight period through changes in phenology. This response is of a similar magnitude to that of animals with a purely terrestrial life cycle and plants (Figure 3.3) suggesting that aquatic and terrestrial life history stages have a similar sensitivity to environmental warming despite that warming being slightly reduced in both rivers (Pilgrim et al., 1998) and lakes (Hostetler and Small, 1999). Patterns seen here in Odonata are likely to be seen in other insects with aquatic stages to their life cycles.

# *Chapter 4. Effects of recorder effort on the detection of range shifts from historical data*

## 4.1. Abstract

Climate-induced range shifts have been detected in a large number of plant and animal taxa and a significant portion of these shifts have been found using records collected over a long period of time. However, the absence of standardised collecting procedures in some historical datasets introduces bias and skew into the data which can result in misleading conclusions. I tested the accuracy of published methods for accounting for this heterogeneity. An extensive, heterogeneous database of sightings of Odonata was analysed using four published methods to control for uneven recorder effort. For each method five different range statistics were calculated. The results were compared and tested against changes in temperature over time to select the most accurate method. Significant variation existed between results derived using different methods and different range statistics. Range statistics were also shown to exhibit different biases to varying recorder effort, particularly those most commonly used in published studies. A combination of existing methods is recommended to control for temporal variation in recorder effort. A novel range statistic based on a gamma distribution, which lacks the inherent bias of existing statistics, is suggested as a descriptor for range margins. Accurate description of past range shifts is essential for correct predictions of future trends and for making decisions concerning conservation priorities.

## 4.2. Introduction

While broad geographic trends such as the decline in biodiversity towards the poles are clearly visible, it is vital that the apparent stasis of these trends does not detract from the dynamic, species-level processes that underlie them. Indeed, the dependence of the global biota upon certain ranges of climatic variables means that, as the climate changes, distributions may also change in a predictable manner. The ability to predict the spatial responses of organisms to climate change plays an important role in planning conservation measures for threatened species (Williams et al., 2005).

Large-scale ecological investigation and prediction is an area which, due to the vast complexity inherent within the field, is particularly susceptible to over-simplifications and misinterpretations. Two approaches which have been used in this field have the potential to provide inaccurate, if alluring, results. The first is the use of "bioclimate envelope models". These models take as their basis the assumption that a species' range is determined by climatic variables. However, this

ignores the contribution of both ecological factors (Davis et al., 1998) and landscape structure (Hill et al., 2001). The debate over this approach has been covered elsewhere (Pearson and Dawson, 2003).

The other approach employed to investigate large-scale distributional changes is that of the ecological census. This can be carried out by monitoring the same study sites as used in previous studies to assess differences between the two time periods (e.g. Sagarin et al., 1999). However, this offers only a regional view on distributional changes. In order to gain an insight into more general trends, researchers have previously turned to historical records (Telfer et al., 2002).

Distributional changes have been documented in a great number of animal and plant species (Parmesan et al., 1999, Hitch and Leberg, 2007, Mieszkowska et al., 2006, Warren et al., 2001, Thomas and Lennon, 1999). When presented with a plethora of biological records with a broad temporal and spatial scope, there is great temptation to draw grand conclusions without fully considering the limitations that such datasets carry (Shoo et al., 2006) and to date no comparison has been made of the variety of methods that have been used. For example, records in a British biological database are usually biased towards later time periods and lower latitudes (Figure 4.1). The spatial bias is likely due to the higher population density at lower latitudes (combined with more amenable environmental conditions for invertebrates). I compare four prominent methods for controlling for uneven recorder effort.

*Method 1 – Resampling (Warren et al., 2001)*

Warren et al. (2001) attempted to equalise the number of butterfly records in each of two time periods (1970-82 and 1995-99) in order to compare shifts in the northern range margin. This range margin was calculated by averaging the northern extents of the 10 most northerly records. Recorder effort was controlled for by randomly subsampling the later, more heavily recorded period so that the same number of records was used in each period. This was carried out separately for each 100km grid square so as to maintain the spatial variation in records.

*Method 2 – Common Squares (Hickling et al., 2005)*

An alternative to resampling was used by Hickling et al. (2005) who simulated a census in two eleven-year time periods (1960-1970 and 1985-1995) to track changes in the range margins of British Odonata. They included in their analysis only those records that were taken from 10km grid squares (the spatial resolution most commonly used in regional analyses) that had been monitored

in both time periods. The range margin was then calculated for each species according to the same marginal-averaging method of Warren et al.

*Method 3 – Threshold Diversity (Hickling et al., 2006)*

In a later analysis, Hickling et al. (2006) augment the Common Squares method by further excluding 10km grid squares that did not have a certain proportion (10% or 25%) of the species of interest recorded. The intention was to control for variation in recorder effort *between* sampled sites as well as controlling for variation in recorder effort in the wider landscape context.

*Method 4 – Regression Intercept (Thomas and Lennon, 1999)*

Finally, Thomas and Lennon (1999) used a method similar to that of Hickling et al. (2005) to derive range margins changes between 1968-72 and 1988-91 for birds. Only records from 100km$^2$ squares that were monitored in both time periods were included in the analysis. Having derived a range shift for each of the species in their dataset, they then plot individual species shifts against the log difference between time periods in the number of 100km$^2$ squares in which that species was recorded. By taking the *y*-intercept of the regression line of this plot, they are able to infer the range shift of a species that had no variation in recorder effort between time periods.

Each of these methods has been used to produce results which have generated high-profile publications but there has been little study of the variation between each of the measures (Shoo et al., 2006). I present a methodological analysis of these four methods used to account for uneven recorder effort in a database of sightings of British Odonata. Using each of the methods I calculate five measures of range shift. I also provide calculations for the threshold at which a species' rarity affects the accurate calculation of range margins.

## 4.3. Methods

### 4.3.1. The British Dragonfly Society database

To illustrate the methodological considerations highlighted above, I use the extensive database of sightings of Odonata maintained by the British Dragonfly Society (BDS). This is a database with extreme spatial and temporal skew in the distribution of records (Figure 4.1). Records were selected from between 1960 and 2004 (n=349,624, as of November 2005), as this represents the period of current warming (Jones and Mann, 2004) and, therefore, the period most heavily analysed in search of changes in distributions. The database contains records of 50 species, of which 38 are residents and 12 are vagrants or migrants.

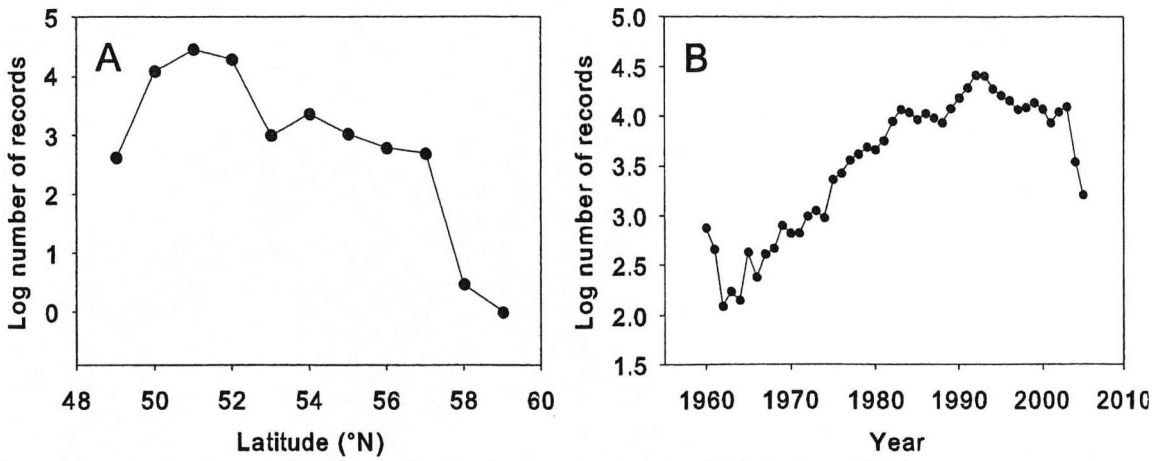


**Figure 4.1 – Variation in recorder effort in the BDS database in relation to (A) latitude and (B) date.**

### 4.3.2. Exclusion of species

Species with highly restricted distributions were excluded. To establish a threshold for exclusion, the relationship between sampling intensity and range margin accuracy was investigated. A hypothetical one-dimensional range of 100 units was sampled at varying intervals: every cell (n=100), every 2nd cell (n=50), every 3rd cell (n=32), etc. The range margin was defined in each case as the mean of the 10 highest cell values with the "correct" range margin being the absolute highest cell value (100). Range margins of samples were expressed as percentages of this correct range margin. The process was repeated for ranges of 200, 300, 400 and 500 units.

The results showed that, regardless of the size of the range, there was a very clear hyperbolic relationship between the number of squares that had been sampled and the accuracy of the range margin result (Figure 4.2; $R^2$ = 98.0%). This relationship was determined using SigmaPlot (v.10). 90% precision was chosen as a threshold that would maintain accuracy whilst retaining the majority of the data. Using the equation of the curve, it was found that 45 sampling points were necessary to generate at least 90% precision, so species lacking records from 45 different 10km grid squares were excluded from the analysis. 15 other species were excluded if they exhibited irregular ranges or geographically constrained distributions (i.e. those that could not expand further).

### 4.3.3. Comparison of methods

I compare the validity and variation in results between four approaches used to control for uneven recorder effort ("methods") and five statistics for describing the location of a species' range ("measures"). Eighteen pairs of time periods were selected to provide coverage of the entire period

as well as a variety of degrees of uneven recorder effort. For each of these, four separate analyses were carried out with different methods: (i) only records from grid squares sampled in both time periods (Hickling et al., 2005), hereafter CSM ("Common Squares Method"), (ii) only grid squares sampled in both time periods that contained 10% of the species of interest (Hickling et al., 2006) hereafter $TD_{10}$ ("10% Threshold Diversity"), (iii) only grid squares sampled in both time periods that contained 25% of the species of interest (Hickling et al., 2006), hereafter $TD_{25}$ ("25% Threshold Diversity") and (iv) random sub-sampling of more heavily recorded period (Warren et al., 2001), hereafter RM ("Resampling Method"). A control was also carried out which did not account for recorder effort in any way, hereafter "NCM" ("No Control Method").

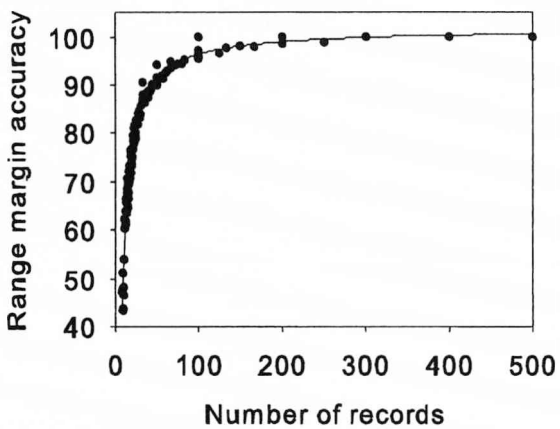


**Figure 4.2 – Hyperbolic relationship between sampling intensity and the accuracy of the range margin estimate.**

For each of these time periods, the range margin was calculated as the mean of the 10 most northerly grid squares in which each species was recorded. For comparison the mean, median and maximum (hereafter "absolute") latitude of the records were also calculated. In addition to these measures, a gamma distribution was fitted to each set of latitudinal data using the *fitdistr* function in the *MASS* library (Venables and Ripley, 2002) in *R* (R Development Core Team, 2006). From this, the 95$^{th}$ quantile was found as an alternative method of estimating the range margin. The advantages of this statistic over existing statistics are twofold: firstly the shape of the gamma distribution includes an element of skew, thereby modelling the poleward tail of the distribution of records (see, for example, Figure 4.1A) more accurately. Secondly an approach based on probability distributions removes the errors associated with absolute numbers of records that are inherent within the absolute and margin measures. The range shift was calculated as the difference between

the values (mean, median, absolute, margin or 95$^{th}$ gamma quantile) of each time period. These were averaged across species to produce a mean range shift within each analysis.

This analysis was carried out twice: once with the raw range shifts as described above and a second time implementing Thomas and Lennon's (1999) "intercept method", hereafter RIM ("Regression Intercept Method"). Only time periods where the regression line crossed the y-axis (i.e. the range of values for log difference in record number included zero) were included in the analysis to insure against extrapolation beyond the data. Differences between methods and measures were tested using a GLM with method, measure and whether the RIM was used as factors in the model. The GLM was fitted with and without the NCM.

### 4.3.4. Comparison of measures

In order to determine which of the potential measures of range location is most robust to the impacts of uneven recorder effort, 7269 records for *Coenagrion puella* (the most heavily recorded odonate species in the BDS database) from between 1960 and 2004 were extracted from the database. The five measures of range location (mean, median, margin, absolute and 95$^{th}$ gamma quantile) were calculated for random sub-samples of the records representing recorder efforts ranging from 1% to 100%. A "range shift" (which in this case would be wholly an artefact of sampling) was estimated as the difference in each measure between each level of recorder effort and the value of that measure at 100% recorder effort.

### 4.3.5. Minimum detectable range shift

To establish which of the measures of variation in geographic range was most sensitive to change, the minimum detectable range shift (δ) was calculated using the methods in Shoo et al. (2006):

$$\delta = \sqrt{\frac{s_d^2}{n}}\left(t_{\alpha(2),v} + t_{\beta(1),v}\right)$$

Where $d$ is the range shift, $s_d^2$=is the variance of sample values of $d$, $n$ is the number of species and $v$=$n$-1. GLM was used to test for differences between the measures and the methods in the minimum detectable range shift.

### 4.3.6. Method-measure validation

To test the validity of each method-measure combination, average annual range shifts (calculated as the mean range shift between two periods divided by the interval between those two periods) were regressed against the average annual change in temperature between those periods (the slope of

the linear regression fit of mean Central England Temperature (CET) on year) and recorder effort (log difference in records between periods). Mean annual temperature change increased with time while recorder effort showed the opposite pattern (Figure 4.3). A method-measure combination that accurately reflects the changing environmental conditions would, therefore, have resulted in a positive, significant relationship with annual temperature increase and a relationship with recorder effort that is not positive and significant.

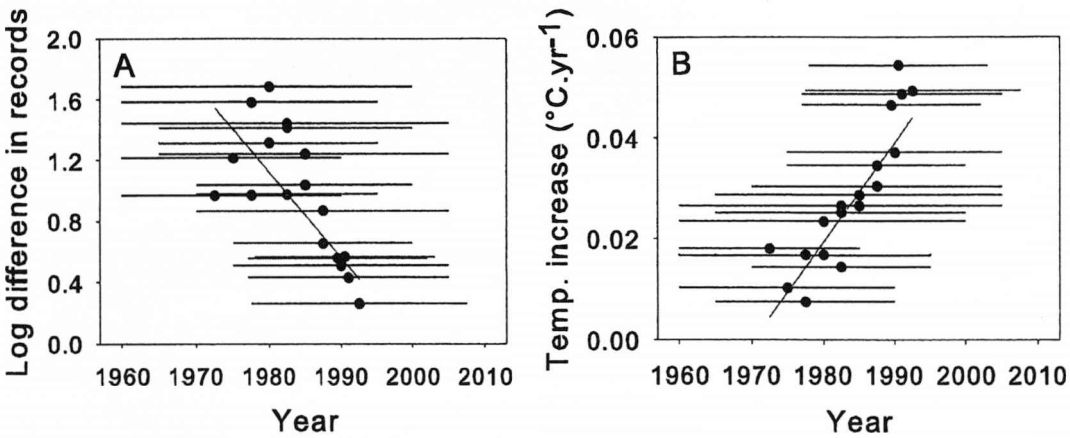


**Figure 4.3 – Variation in (A) sampling effort (log difference in records between the two sampling periods) (linear regression: $F_{1,16}$=30.1, p<0.001, $R^2$=63.2%) and (B) the rate of temperature increase (linear regression: $F_{1,16}$=46.3, p<0.001, $R^2$=72.7%) between different sampling periods. In each case circles represent the mid-point of the sampling periods and the horizontal lines are the extent of the periods.**

## 4.4. Results

### 4.4.1. Comparison between methods

RIM, method and measure were significant factors in determining mean annual range shift when the NCM was included (RIM, $F_{1,595}$=28.85, p<0.001; method, $F_{4,595}$=43.13, p<0.001; measure, $F_{4,595}$=39.85, p<0.001; $R^2$=0.374) and when NCM was excluded (RIM, $F_{1,471}$=34.28, p<0.001; method, $F_{3,471}$=6.85, p<0.001; measure, $F_{4,471}$=27.55, p<0.001; $R^2$=0.249). However, the similarity of the raw and RIM data in Figure 4.4 and the strong correlation between raw and RIM values (r=0.714, p<0.001) suggests that the RIM simply reduces the magnitude of detected shifts.

### 4.4.2. Comparison between measures

When recorder effort was varied, estimation of the range margin using the margin measure exhibited a significant, directional skew (Figure 4.5A). This results in an apparent range shift which increases exponentially as the percentage of included records decreases, leading to the linear relationship seen on the log-linear plot at the top-left of Figure 4.5A. Estimation of the range margin using the absolute measure shows a similar pattern at highly uneven recorder efforts (1% - 30 % of records included; Figure 4.5B). However, this method is extremely accurate at more even recorder effort (i.e. once the correct extreme value has been identified within the sub-sample). This accuracy is likely to be extremely random in nature.

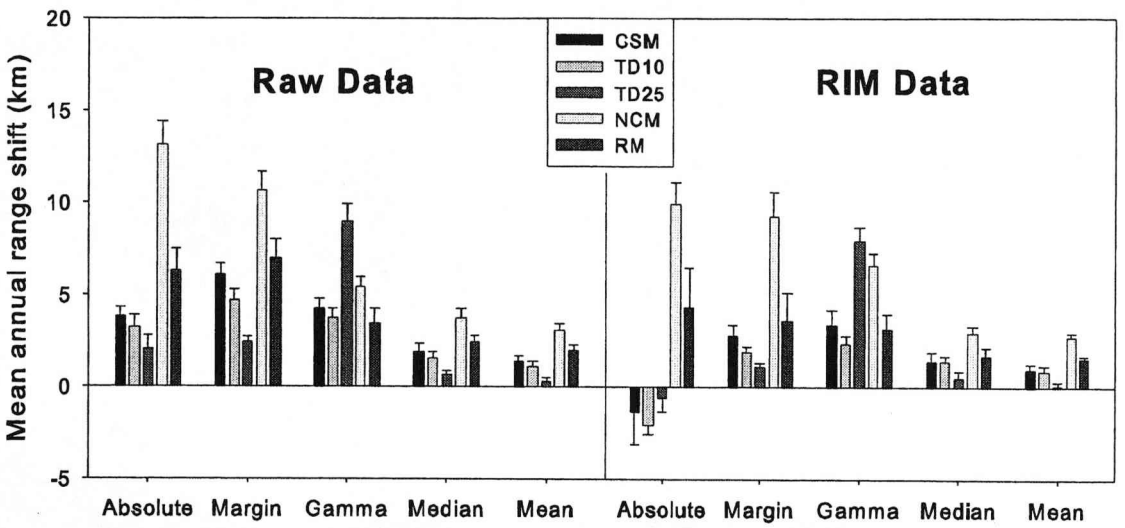


**Figure 4.4 – Comparison between mean annual range shifts averaged across all analyses for each combination of method and measure, before and after the Thomas and Lennon (1999) intercept method was applied. CSM=Common Squares Method, TD10=10% Threshold Diversity, TD25=25% Threshold Diversity, NCM=No Control Method, RM= Resampling Method (see text for details).**

Mean, median and 95$^{th}$ gamma quantile each responded similarly, showing no artefacts due to recorder effort. The *ncv.test* function in the *car* library (Fox, 2002) in *R* was used as a post-hoc test of equality of variance in these three measures. Variance was constant across recorder effort for mean ($\chi^2$=0.615, p=0.433; Figure 4.5C) and median ($\chi^2$=0.068, p=0.794; Figure 4.5D) but varied with recorder effort in the 95$^{th}$ gamma quantile ($\chi^2$=17.561, p<0.001; Figure 4.5E). This non-constant variance results from a more accurate approximation of the "true" range shift at higher recorder

effort (although it is worth noting that the change in the error is relatively small, even accounting for the log scale in Figure 4.5E).

### 4.4.3. Minimum detectable range shift

The minimum detectable range shift varied significantly between methods and measures (ANOVA: method, $F_{4,396}=3.42$, $p=0.009$; measure, $F_{4,396}=181.31$, $p<0.001$; see also Figure 4.6). The difference between the mean record location provided the most sensitive measure of shifts in range (22.13km ±1.12 (mean ±SE)), followed by median (25.17km ±1.23), 95$^{th}$ gamma quantile (54.16km ±2.25), margin (68.62km ±3.18) and then the absolute range limit (113.54km ±4.62). The method which produced the lowest minimum detectable range shift was the RM.

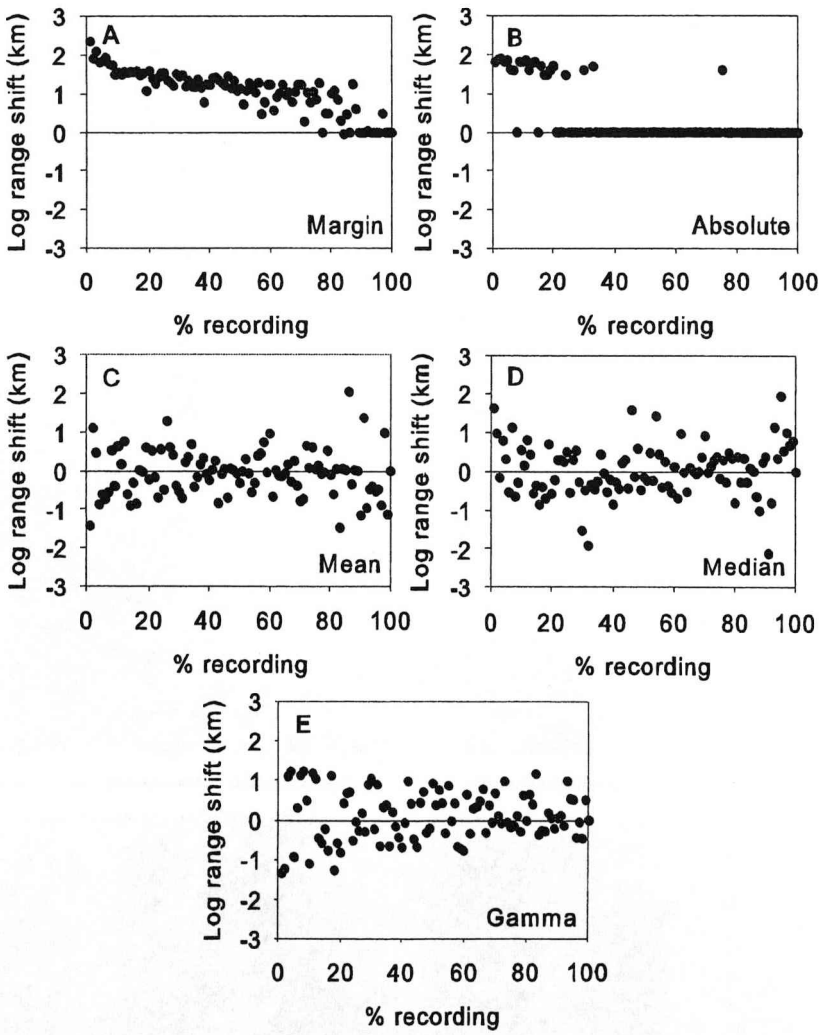


**Figure 4.5 – Impact of recorder effort on artefacts in range shift calculations using different measures of range location. See text for details.**

### 4.4.4. Method-measure validation

Of the 25 analyses of range shifts that were conducted, only two resulted in a significant, positive relationship with annual rate of temperature increase and a relationship with recorder effort that was not significant and positive (Table 4.1). One of these five methods (RM with the margin measure) has been used in the literature (Warren et al., 2001). The 95$^{th}$ gamma quantile measure, which has not been used before, produced the other method-measure combination in which the desired relationships were obtained.

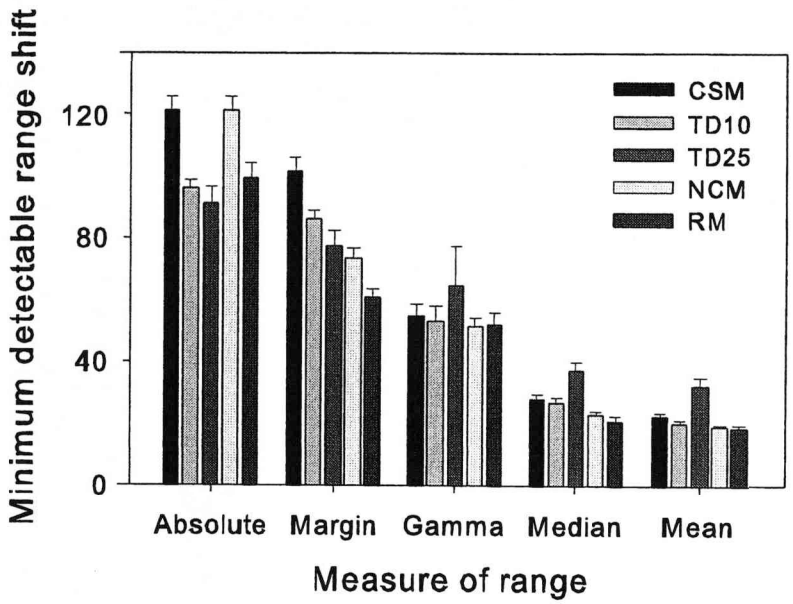


**Figure 4.6 – Minimum detectable shifts in four measures of geographic distribution calculated by five different methods (see text for details). Error bars are 1SE.**

It is important to note that $TD_{25}$ resulted in a relatively small number of species being included in analyses and only half of the 18 analyses containing any species at all. The results for $TD_{25}$ in Table 4.1, Figure 4.4 and Figure 4.6 should be viewed with this in mind, although they are included for completeness.

### 4.4.5. Selected model results

The two models highlighted in Table 4.1 as fulfilling the intuitive criteria of an accurate method-measure combination give mean annual range shifts across the entire period of 3.41km.yr$^{-1}$ ±0.815 (RM gamma) and 6.96km.yr$^{-1}$ ±1.03 (RM margin). When the RIM is applied, these are reduced to 3.103km.yr$^{-1}$ ±0.840 (RM gamma) and 3.59km.yr$^{-1}$ ±1.53 (RM margin). Note that the margin measure

is halved in magnitude whereas the gamma measure is not significantly affected by further controls for recorder effort, suggesting that the method based on the gamma measure is already robust.

**Table 4.1 – Results of multiple regressions of the log difference in the number of records in each analysis ("Records") and the mean annual change in temperature between the periods ("Temp") on the mean annual range shift. Rows highlighted in grey are those method-measure combinations conforming to the criteria for accurate range shift measurement. Values are t-statistics and *=p<0.05.**

| Method | Measure | Records | Temp | $r^2$ |
|---|---|---|---|---|
| CSM | Absolute | -1.83 | -0.89 | *9.0* |
| | Margin | -3.17* | 0.17 | *54.2* |
| | Mean | -2.15* | -0.37 | *23.8* |
| | Median | -2.11 | -1.14 | *13.9* |
| | Gamma | -3.17* | -0.49 | *45.9* |
| $TD_{10}$ | Absolute | -3.42* | -4.36* | *50.3* |
| | Margin | -3.68* | 0.13 | *61.3* |
| | Mean | -1.88 | 0.07 | *24.7* |
| | Median | -1.86 | -0.47 | *14.8* |
| | Gamma | -2.22* | -0.51 | *23.5* |
| $TD_{25}$ | Absolute | 3.81* | 3.78* | *63.1* |
| | Margin | 1.30 | 1.61 | *7.1* |
| | Mean | 0.92 | -0.84 | *48.6* |
| | Median | -0.84 | -1.06 | *0.0* |
| | Gamma | -0.52 | -0.00 | *0.0* |
| RM | Absolute | -1.98 | 1.70 | *55.9* |
| | Margin | -2.80* | 2.17* | *70.7* |
| | Mean | -3.01* | -0.01 | *48.9* |
| | Median | -2.66* | -1.15 | *26.8* |
| | Gamma | -2.04 | 2.41* | *65.5* |
| NCM | Absolute | -2.49* | -3.44* | *36.7* |
| | Margin | -2.44* | -3.62* | *39.5* |
| | Mean | -5.88* | -8.47* | *80.4* |
| | Median | -4.51* | -7.42* | *76.1* |
| | Gamma | -3.03* | -0.53 | *42.4* |

## 4.5. Discussion

Historical databases of sightings of animals and plants are a valuable resource in detecting spatial and temporal change. However, the inherent biases that are found in such datasets require special

methods to produce meaningful results. I present the first comparison of methods used to detect range margin changes in historical data and demonstrate that their reliability varies markedly.

In a comparison of methods I found the Resampling Method of Warren et al. (2001) to be the least vulnerable to bias from uneven recorder effort. This method showed no positive variation with recorder effort and best reflected the increasing rate of warming across the time periods under consideration. On top of this control for sampling effort across the landscape, the Regression Intercept Method of Thomas and Lennon (1999) should be used to account for changes in individual species sampling between periods. Although this removes the ability to detect individual species' range shifts, it adds power to the detection of taxon-wide effects.

I also gave consideration to which range statistic should be used when comparing distributions in two different time periods. The obvious statistic would simply be the most extreme record. However, it is clear that for the majority of cases where data are not systematically collected this will be subject to stochasticity and extremely sensitive to uneven recorder effort (Figure 4.5B). Calculating the margin by averaging the 10 most extreme locations accounts for this to a certain extent and is widely used in the literature (Warren et al., 2001, Hickling et al., 2006, Hickling et al., 2005, Thomas and Lennon, 1999). However, I showed that this also results in artefacts resembling range shifts in datasets where none is present (Figure 4.5A).

Detection of shifts in range using the mean and median records have rarely been used, although the mean record has been shown to have a greater sensitivity to change than the absolute range margin in surveys of mountain bird assemblages (Shoo et al., 2006). I found a similar effect, with the mean and median records providing a much more sensitive measure of change compared to the absolute or margin measures. However, such a measure fails to pass intuitive tests of its validity such as correlations with the rate of change of temperature.

I found support for an alternative method for the detection of trends in range margin shifts using the 95$^{th}$ quantile of a fitted gamma distribution. Due to the capacity of the gamma distribution to incorporate elements of skew into its shape, fitting a gamma distribution to each dataset individually more accurately accounts for the frequency distribution of the records. This includes a portion of the latitudinal variation in recorder effort shown in Figure 4.1A. Although the error associated with this measure increases at higher levels of uneven recorder effort, the error lacks the directional bias associated with the absolute and margin measures. For this reason, I recommend

the use of frequency distribution approaches in the measurement of range shifts in preference to those currently in use.

The rate of warming over the period that has been considered in this analysis (1960-2005) can be estimated by regressing the Central England Temperature (CET) on date to give a gradient of 0.027°C.yr$^{-1}$. It has been estimated that a 1°C rise in temperature is equivalent to a 150km shift in isotherms (Intergovernmental Panel on Climate Change (IPCC), 1996), which gives an annual isotherm shift of 4.05km.yr$^{-1}$. This is comparable to – if slightly greater than – the shifts predicted from the selected method-measure combinations with RIM presented above (3.103km.yr$^{-1}$ ±0.840 (RM gamma) and 3.59km.yr$^{-1}$ ±1.53 (RM margin)).

Since climate has varied in the past (particularly during the early Quaternary period (Adams et al., 1999)), it might be expected that extant organisms would possess some form of adaptation which permitted their survival in the face of such change (Balmford, 1996). Indeed, dispersal rates during the Quaternary climate fluctuations were surprisingly high and compensated for changing climate (Clark et al., 1998, Ashworth, 1997).

The consistency of range shift results across multiple taxa (Parmesan and Yohe, 2003) suggests that the observed trend in poleward movements is not an artefact of detection methods. Long-distance dispersal plays a substantial role in maintaining this process and is vital for the persistence of metapopulations (Trakhtenbrot et al., 2005). However, it is likely that we have underestimated the maximum dispersal ability of species as this parameter is difficult to measure in standard mark-release-recapture (MRR) studies (Thompson and Purse, 1999, Slatkin, 1985, Schneider, 2003). Further work is needed to quantify dispersal and attempt to account for biases involved with study area size.

However, the ability of organisms to disperse or adapt in the face of contemporary climate change may be compromised by the sheer rate of warming coupled to reduced permeability of the landscape (Davis and Shaw, 2001, Travis, 2003, Opdam and Wascher, 2004). This possibility is also suggested by the results of this study with estimates of past rates of poleward movement of British Odonata (3.103km.yr$^{-1}$ ±0.840 or 3.59km.yr$^{-1}$ ±1.53) being slightly lower than the velocity of poleward isotherm movement (4.05km.yr$^{-1}$). As a result, conservation measures are being specifically targeted towards facilitating dispersal (Williams et al., 2005, Araújo et al., 2004). This

also places an emphasis on landscape-scale conservation strategies designed to maintain the connectivity between habitat patches.

## 4.6. Conclusions

While each of the methods previously used to control for the effects of uneven recorder effort in historical datasets appears reasonable, those methods vary in their ability to accomplish that task. Based on an analysis of an extensive and heterogeneous historical dataset, I recommend a combination of sub-sampling of more heavily recorded periods and a frequency distribution approach to range margin description. With a large amount of historical data potentially still unanalysed, this study should act as a cautionary tale to those who might wish to embark on such analyses.

# *Chapter 5. The impact of climate-induced distributional changes on the validity of biological water quality metrics.*

## 5.1. Abstract

I present data on the distributional changes within an order of macroinvertebrates used in biological water quality monitoring. The British Odonata (dragonflies and damselflies) have been shown to be expanding their range northwards and this could potentially affect the use of water quality metrics. The results show that the families of Odonata that are used in monitoring are shifting their ranges poleward and that species richness is increasing through time at most UK latitudes. These past distributional shifts have had negligible effects on water quality indicators. However, variation in Odonata species richness (particularly in species-poor regions) has a significant effect on water quality metrics. I conclude with a brief review of current and predicted responses of aquatic macroinvertebrates to environmental warming and maintain that caution is warranted in the use of such dynamic biological indicators.

## 5.2. Introduction

Freshwater systems are vital for life and the strain that increasing human population densities place upon them means that careful monitoring is required to avoid over-exploitation (Dudgeon et al., 2006, Chapman, 1996). Biological monitoring of rivers has been used in Europe for over 100 years (see Hawkes, 1997, for a history of biological monitoring, particularly in Britain) but it is only in the past 40 years that Britain has adopted such a system to compliment other forms of environmental monitoring.

The monitoring scheme in use in Britain consists of a set of families of macroinvertebrates which are scored from 1 to 10 based on their sensitivity to pollution (Biological Monitoring Working Party, 1978; hereafter "BMWP"). The scores for all families present in a given stretch of river are totalled and then divided by the number of contributing families to find an average score per taxon (ASPT). This value is then compared to an ideal, "pristine" ASPT generated using the river invertebrate prediction and classification system (RIVPACS; Moss et al., 1987). Since the original scheme was designed, scores for each taxon have been revised in light of computer analyses by Walley and Hawkes (1996, 1997), leading to a reduction in the uniformity of scores between same-order families.

There are a number of issues arising from this system of biological monitoring; chiefly that different pollutants have different effects on each taxon (Moss, 1998). However, another potential confounding factor that has arisen from recent research is the changing distributions of those organisms that contribute to the BMWP scores. A wide range of freshwater macroinvertebrates have been shown to be responding spatially to climate change (Burgmer et al., 2007, Hickling et al., 2006, Heino, 2002).

Included among these macroinvertebrates are the Odonata (the dragonflies and damselflies) which, being of tropical origin (Pritchard and Leggott, 1987), are potentially sensitive to environmental warming (e.g., Hassall et al., 2007, Hickling et al., 2006). However, the Odonata have also been identified as being sensitive to a range of pollutants and are used as indicators of water quality both within the BMWP system and elsewhere (Menetrey et al., 2005, Foote and Hornung, 2005, Clark and Samways, 1996).

This study will test whether changes in the distributions of odonate families have varied sufficiently over the current period of warming as to introduce an error into calculations of water quality that are based on their presence/absence. I then conclude with a discussion concerning the merits of the use of this taxon and other macroinvertebrates in the monitoring of water quality in light of widespread responses to environmental warming.

## 5.3. Methods

The British Dragonfly Society maintains an extensive dataset of records of British Odonata. This database contains reported sightings of larvae, adults and exuviae of resident and immigrant odonates in the UK dating back to the early 19$^{th}$ century. Most of the ca. 270,000 records are concentrated at lower latitudes and between 1980-2000 (for more details, see Hassall et al., 2007). Each species in the database was coded according to its family. The presence of each species and each of the seven families contained in the BMWP scores (Aeshnidae, Coenagrionidae, Calopterygidae, Cordulegastridae, Lestidae, Libellulidae and Platycnemidae) was then tested for in 1° latitudinal bands across England, Wales and Scotland, from 50°N to 60°N, and, within those geographical areas, in time periods from 1960-4, 1965-9, 1970-4, 1975-9, 1980-4, 1985-9, 1990-4 and 1995-9.

The years from 2000-04 were excluded because of doubts over the completeness of the database. The Corduliidae (*Somatochlora metallica*, *S. arctica* and *Cordulia aenea*) and Gomphidae (*Gomphus*

*vulgatissimus*) are excluded from the analysis because they are not found in the BMWP scores. Also, these species are all relatively rare and exhibit highly fragmented distributions.

The ASPT for the Odonata was calculated for each combination of latitude and time using the revised BMWP scores in Walley and Hawkes (1996). The simplifying assumption was made that all species present in a latitude-time combination were present throughout that combination. The BDS database is biased both temporally and spatially in terms of recorder effort and so the number of records was also noted for each combination. The species richness and the ASPT were then analysed in an ANCOVA with latitude and time as factors and the log of record number as a covariate. A model of exponential increase to a maximum was fitted to the ASPT data with respect to species richness.

In addition to this, a range shift analysis was performed (as per the methods in Hickling et al. (2005)) for the seven families to estimate the extent of movement over the period of sampling. Previous concerns have been raised about the impact of unbalanced recorder effort between two periods in an analysis such as this (Shoo et al., 2006), so the range shift results were analysed using non-parametric statistics (Spearman's rank correlation; because of the small sample size, $n$=7) to look for an impact of recorder effort.

## 5.4. Results

The number of species recorded at each latitude/time combination was highly significantly correlated with the log of the number of records for that combination ($r$=0.918, p<0.001). The GLM of species richness showed that there was a significant effect of both latitude and time when recorder effort (log number of records) was controlled for (latitude: $F_{10,69}$=214.25, p<0.001; time: $F_{7,69}$=20.28, p<0.001, Figure 5.1). This result was also found when ASPT was analysed, although the significance was not so strong (latitude: $F_{10,69}$=20.84, p<0.001; time: $F_{7,69}$=2.86, p=0.011).

Figure 5.2 shows a comparison between the temporal variation in species richness across a latitudinal range and the variation in ASPT across the same temporal and spatial scale. It is clear from this figure that the trend in ASPT, although statistically significant, does not mirror the changing species richness. The fit of the model of exponential growth to an asymptote was highly significant ($F_{2,83}$=85.02, p<0.001). At low species richness the odonate ASPT is relatively low and it is not until species richness increases that this equilibrates.

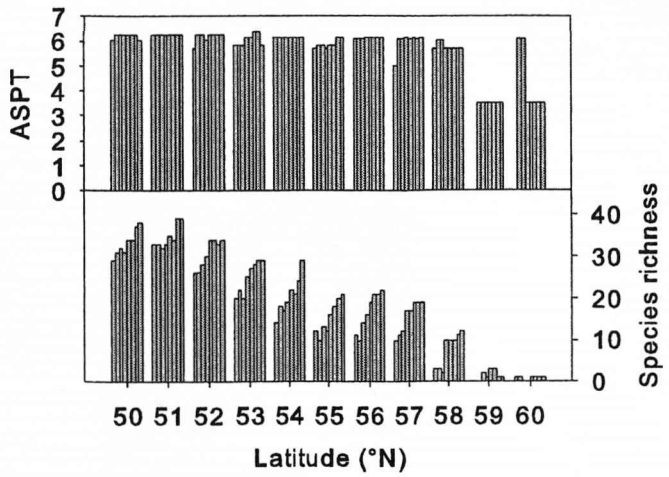


**Figure 5.1 – A comparison between temporal and latitudinal variation in water quality metrics (average score per taxon – ASPT, top), and in species richness (below). Bars within each latitudinal band represent, from left to right, the time periods 1960-64, 1965-69, 1970-74, 1975-79, 1980-84, 1985-9, 1990-94 and 1995-99.**

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The range shift analysis suggested a consistent poleward shift in all seven families (Table 5.1). Spearman's rank correlation analyses of range shifts and recorder effort showed no significant correlations between (i) absolute difference in record number ($\rho$=-0.464, p=0.294), (ii) log difference in record number ($\rho$=-0.571, p=0.180) or (iii) ratio of record numbers ($\rho$=-0.571, p=0.180). It is thus concluded that the shifts in distribution are real and not an artefact of recording bias.

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**Table 5.1 – Poleward range shifts of the northern range margins of each of the seven Biological Monitoring Working Party odonate families between 1960 and 1999.**

| Family | Range shift (km) |
|---|---|
| Aeshnidae | 70 |
| Calopterygidae | 89 |
| Coenagrionidae | 19 |
| Cordulegastridae | 53 |
| Lestidae | 175 |
| Libellulidae | 38 |
| Platycnemidae | 55 |

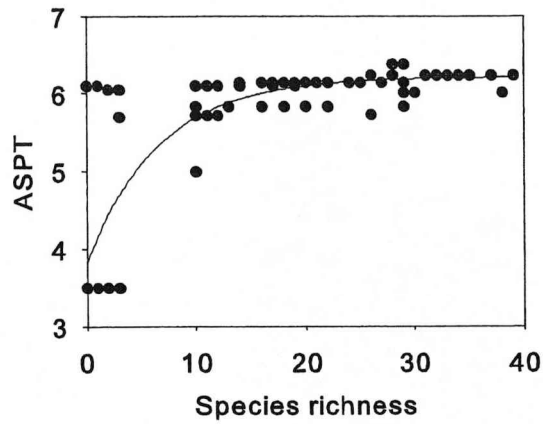


**Figure 5.2 – Variation in average score per taxon (ASPT) with increasing species richness. Fitted model is an exponential rise to a maximum ($R^2$=66.4%).**

## 5.5. Discussion

The range margins of British Odonata have been shown to be advancing poleward. This is thought to be a response to increases in environmental temperature and subsequent increases in amenable habitat at the poleward range margin. However, this study has shown that these changes in the distributions of both individual species and higher order taxonomic groups have not impacted on the portion of water quality metrics (as defined by the BMWP) contributed by the Odonata. Despite this result, it is important to note that there are some highly species-poor regions of Scotland (between 59°N and 61°N) which could soon be colonised by a much wider range of Odonata. These regions stand out from the rest of Britain as having particularly low odonate ASPT scores. Indeed, the band from 58°N to 59°N contained only 2 or 3 species until 1975-9 when the number leapt to around 10 species (Figure 5.1).

At these low levels of species richness, a potential error enters into the data. It is unlikely that the low ASPT values at higher latitudes are the result of pollution, as the population densities in those regions are far lower than those at lower latitudes. Instead, odonate populations inhabiting higher latitudes happen to be largely Coenagrionidae (e.g. *Pyrrhosoma nymphula* and *Ischnura elegans*), which have a low BMWP score. Under predicted range shifts, other taxa will invade those regions, causing an increase in ASPT and, as a result, an apparent increase in water quality.

There are two potential problems with the use of Odonata as indicators of water quality. Firstly, while this taxon appears to favour water bodies that contain relatively low levels of pollutants, a small number of species have been shown to tolerate relatively high levels of some substances (see

Corbet, 2004 chapter 6 for a review). However, sensitivity to organic pollution is almost ubiquitous in the order and this makes them ideal as indicators of this kind of pollution (Menetrey et al., 2005).

A second complicating factor with Odonata (and, potentially, other aquatic macroinvertebrates) is their reported propensity for using different types of habitat in different parts of their range (Buchwald, 1989, Buchwald, 1995, as cited in Corbet, 2004). A variation in habitat use between core and marginal sites within a species' range has been documented in Lepidoptera (Roy and Thomas, 2003) and this phenomenon requires more study in other taxa.

The classification in the BMWP scores is at the level of the family which serves to pool species that exhibit particular habitat associations such as habitat structure and hydrology. The RIVPACS scheme has been highlighted in this study as an example of a scheme that uses macroinvertebrate communities in determining water quality. Despite that fact that relatively few of the British Odonata are obligate rheophiles, a large proportion of British species also make use of lotic habitats as well as their more typical lentic habitats. These two facts combined with the high density of recording of Odonata in the UK make this taxon ideal as an exemplar for other taxa undergoing similar climate-induced change.

A large amount of criticism has been levelled at the use of species distribution models and their application in predicting future ranges based on changing climate (Pearson and Dawson, 2003). This criticism stems from the fact that they only consider abiotic factors. A similar problem besets the current state of biological indicators of water quality: there is more to their habitat requirements than simply more or less pollution.

It is worth pointing out that, although the Odonata have been the focus of this study, similar poleward shifts in distributions have been reported in British aquatic bugs (Hickling et al., 2006). Climate has also been implicated in the determination of species richness of Plecoptera, aquatic beetles and Odonata in Scandinavia (Heino, 2002), in agreement with work by Burgmer et al. (2007), who also add Diptera to the list. These five groups (Odonata, Coleoptera, Hemiptera, Plecoptera and Diptera) comprise 35 out of 81 families in Walley and Hawkes' (1996) revised BMWP scores, suggesting that the impact of climate-induced range shifts on biological water quality indices may need to be assessed in all groups of interest.

The Plecoptera are worth highlighting, since they have been allocated some of the highest BMWP scores. This group has been shown to be "cold-adapted" (Pritchard and Leggott, 1987) and its species richness declines with increasing temperature (Heino, 2002, although cf. Burgmer et al., 2007). This means that, while other invertebrate taxa may exhibit an increase in species richness, the number of Plecoptera species at a given site is likely to decrease. If this predicted decline in species richness is mirrored by a decline in family-richness then the ASPT for a given site would decline.

The net effect of boreal taxa becoming extinct in the south of their range and colonisation of the same regions by southern species as a result of climate-induced shifts in their fundamental niches requires further investigation. While the effects of warming on confounded by changes in river quality and discharge (Durance and Ormerod, 2008), there is still the potential for the introduction of errors in water quality estimation resulting from such range shifts. The problem of shifting distributions could be circumvented by a simple measure: the redefinition of the RIVPACS standards at regular intervals to ensure that it is representative of the macroinvertebrate communities of the "pristine" sites, thereby controlling for the state of current climatic flux. This analysis has shown a relatively rapid increase in species richness of odonate species at a range of latitudes, but the ASPT metric has remained robust. If other orders show similarly small changes in ASPT then there is no need to update the RIVPACS scheme frequently. However, the repetition of such a survey would be of immense interest to those studying community composition and environmental change.

## 5.6. Conclusions

The Odonata (dragonflies and damselflies) have exhibited poleward shifts in their northern range margin. Projected changes in distribution and concurrent increases in species richness will affect indices of water quality (ASPT). Care must be taken when using biological indicators of water quality to acknowledge and accommodate the dynamic nature of species' ranges under climate change. Many of the taxa used in the BMWP scheme have been shown to be responding to climate change (Hickling et al., 2006) and the continuation of the current trend in distributional change may still result in artefacts in these metrics, if they are not already apparent. Since the method outlined above for the monitoring of water quality in streams and rivers was influential in the generation of the Water Framework Directive (European Commission, 2000), this is a potentially wide-reaching issue.

# *Chapter 6. Variation in morphology between core and marginal populations of three British damselflies*

## 6.1. Abstract

As selective pressures are altered by the changing climate, species have been shown to shift their distributions. Here I investigate morphological variation in dispersal-related traits between core and marginal populations in three species of Odonata, a taxon that is known to be expanding polewards. I sampled individuals of (i) *Calopteryx splendens*, a species with a rapidly expanding range, (ii) *Erythromma najas*, a species with a slowly expanding range, and (iii) *Pyrrhosoma nymphula*, a species that does not exhibit a range margin in the UK (as a control). Only *C. splendens* exhibited consistent trends within two dispersal-related traits (wing:abdomen length ratio and aspect ratio). This result suggests that proximity to range margin alone does not account for variations in damselfly morphology, but that the rate of range expansion may also be important in determining variation.

## 6.2. Introduction

There is little doubt that global temperatures are increasing (Karl and Trenberth, 2003) and predictions are that the rate of this warming will increase (Intergovernmental Panel on Climate Change (IPCC), 1996). A number of studies have documented the biological impacts that this climate change has had thus far (Parmesan and Yohe, 2003, Walther et al., 2005). One of the best-documented results of increased environmental temperature is the shift in geographical distirbutions exhibited by a range of species (Hickling et al., 2006), supposedly caused by changes in the location of the fundamental niche.

Individual species shift their ranges through a complex combination of colonisations and extinctions (Holt and Keitt, 2000). When the probability of colonisation and persistence is sufficiently high, new habitats can be colonised by individuals from within the existing range boundaries. However, the individuals that colonise new habitat patches are likely to be an unrepresentative sample of the population from which they disperse (Simberloff, 1981). It might be expected that individuals that found new colonies possess traits which increase the likelihood of successful dispersal. The progeny of those initial colonisers inherit those dispersal traits and make it more likely that subsequent colonisation will occur.

This scenario predicts a capacity for accelerating range expansion and has been demonstrated in the invasion of Australia by the cane toad, *Bufo marinus* (Amphibia), (Phillips et al., 2006) and in British Orthoptera (Thomas et al., 2001). Lepidoptera have also been shown to exhibit some enhanced dispersal-related traits at range margins compared to the core of ranges, including higher body mass, larger thoraces relative to total body mass and lower wing aspect ratios at recently colonised sites (Hill et al., 1999a). Part of the adaptation to dispersal occurs not in exaggerating dispersal-related traits but in reducing traits that are not related to dispersal. In insects, the abdomen is largely reproductive in function and can constitute a significant proportion of the animal's mass. Reducing this mass results in a lower wing loading and, therefore, a greater capacity for dispersal.

The Odonata represent an order of insects which has recently been shown to be responding to climate change by advancing its phenology (Hassall et al., 2007, Dingemanse and Kalkman, 2008) as well as expanding its range poleward in the UK (Hickling et al., 2005), elsewhere in Europe (Ott, 2007, Flenner and Sahlén, 2008) and Japan (Aoki, 1997). This is not surprising given both the aerial nature of its dispersal mechanism and the intimate links that the group has with temperature, including a tropical origin (Pritchard and Leggott, 1987).

In this study I describe morphological variation pertaining to dispersal in three species of British damselfly with different range margin characteristics. Wing length is a reliable proxy for body size in damselflies (Cordero, 1994) as well as in insects in general (Southwood, 1968) and there is evidence that larger species disperse further than smaller species (Conrad et al., 1999). However, the absence of geometric similarity among species makes these comparisons equivocal (May, 1981). The biomechanics of odonate flight have been studied in detail (Rüppell, 1989, Wakeling and Ellington, 1997a, b, c) but this has rarely been related to the ecology of the species (Grabow and Rüppell, 1995). Intraspecific studies of odonate flight morphology have focused on sexual selection and mating success and have not demonstrated variation in dispersal traits (Tsubaki and Ono, 1987, Marden and Waage, 1990). However, decreases in wing loading (or the related wing disk loading) are predicted to increase lift production (Marden, 1987) and high wing aspect ratio could provide greater mass-specific lift at cold temperatures (Azevedo et al., 1998) and has been shown to correlate with greater flight speed in butterflies (Dudley and Srygley, 1994).

I selected three candidate species to represent (i) an expanding range margin, (ii) a static range margin and (iii) variation on a similar latitudinal scale within a range. Using the British Dragonfly Society's database of sightings and the methods described in Hickling et al. (2005), I calculated the

range shifts of all British Odonata over 18 time periods and found the mean annual shift for each species. I selected *Calopteryx splendens* (mean shift = 12.8km.yr$^{-1}$) as the expanding species, *Erythromma najas* (mean shift = 3.6km.yr$^{-1}$) as the slowly expanding species and *Pyrrhosoma nymphula* (mean shift = 1.3km.yr$^{-1}$). It is worth noting that *P. nymphula* has not expanded its range but that the apparent shift is a consequence of the methods used to calculate the range margin. I tested the hypothesis that the species exhibiting the most rapid expansion would possess the most exaggerated dispersal traits.

## 6.3. Methods

### 6.3.1. Sampling

Sites were selected to represent the core and margin of the three species' distributions in the UK (see Figure 6.1 and Table 6.1). The exception is *P. nymphula*, for which sites were chosen to give an equivalent latitudinal difference. Body size declines through the flight season (Banks and Thompson, 1985b) and so sites were visited over as short a space of time as possible to minimise this effect (Table 6.1). Phenology is retarded at higher latitudes and so sampling the northern sites after the southern sites partially accounted for this. Thirty males and thirty females were caught using a butterfly net from each pair of sites and kept in a coolbox until analysis.

**Table 6.1 – Locations of sampling sites and ordinal dates (days since 1st January) on which they were sampled.**

| | Core sites | | | Marginal sites | | |
|---|---|---|---|---|---|---|
| Species | Latitude | Longitude | Sampling date | Latitude | Longitude | Sampling date |
| *C. splendens* | 51.356°N | 0.888°W | 175-179 | 55.092°N | 1.704°W | 185-187 |
| *E. najas* | 51.330°N | 0.822°W | 166-174 | 53.214°N | 2.594°W | 178-181 |
| *P. nymphula* | 50.957°N | 0.978°W | 176-179 | 56.734°N | 3.023°W | 190-191 |

### 6.3.2. Measurements

An attempt was made to sample the specimens non-destructively and so measurement of the specimens required anaesthesia. Chilling was selected for three reasons: (i) some studies have suggested that chilling is preferable to carbon dioxide anaesthesia (Barron, 2000), (ii) delivering consistent bouts of gaseous anaesthetic proved to be difficult and (iii) transporting nitrogen or carbon dioxide gas cylinders was not feasible.

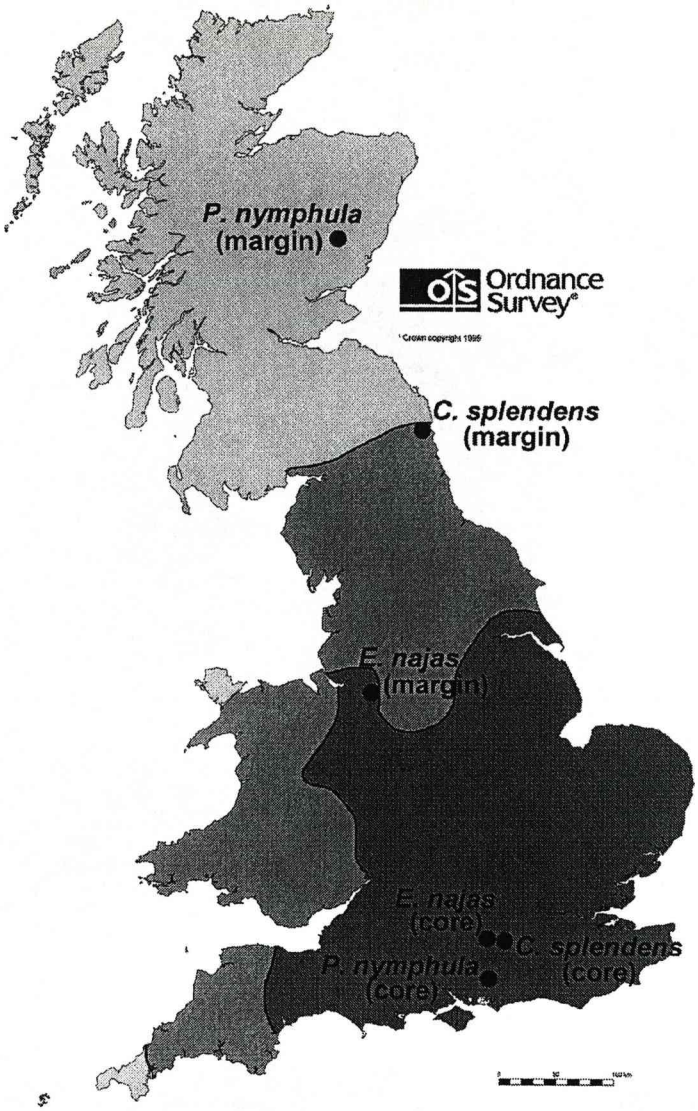


**Figure 6.1 – Map showing locations of core and margin sampling sites in relation to the ranges of the three species. Ranges are concentric such that the range of *Calopteryx splendens* encompasses that of *Erythromma najas* and *Pyrrhosoma nymphula* encompasses both of the other species. Dark grey shows range of *E. najas*, middle grey shows range of *C. splendens* and light grey shows range of *P. nymphula*.**

As soon as possible after capture the individuals were removed from their bags and anaesthetised by chilling at approximately -18°C using a *Lec* U5006W tabletop freezer. The time required for adequate anaesthesia of each species varied and was determined during pilot studies. These times were 60 seconds for *P. nymphula*, 90 seconds for *E. najas* and 150 seconds for *C. splendens*.

Lateral and dorsal scans of all specimens were taken using a Canon Canoscan LiDE 25 flatbed scanner. Specimens were immobilised using microscope slides. The resulting images were analysed

in ImageJ (Rasband, 1997-2007) to find the wing length and wing area of all four wings and abdominal length. Wing length was defined as the length from the costal end of the vein separating the arculus from the discoidal cell to the tip of the wing. It was not possible to take the area of the whole wing due to interference in the scan from the body, so the wing area excluded the portion defined by the junction of the first antenodal cross-vein and the costa, the margin of the arculus and across the anal crossing to the analis.

### 6.3.3. Analysis

The raw measurements were used to calculate two key dispersal traits: wing loading and aspect ratio. Since mass could not be measured accurately on live specimens, an index of flight ability was calculated using the ratio of right forewing length (WL) to abdomen length (AL). This index is similar to that used in studies on *Drosophila* and is inversely related to wing loading (Barker and Krebs, 1995). Aspect ratio was calculated for both hind- and forewings as the square of the wingspan divided by the area. This was averaged across fore- and hindwings to give a mean aspect ratio.

A GLM was used to investigate variations between species, sites and sexes in body size (forewing length) and both of the dispersal traits. An interaction term of gender×site was added. Two-sample, two-tailed *t*-tests were used to test for differences between sites within each sex for each species. To account for the relatively large number of tests being performed (18 t-tests), a Bonferroni correction was applied by multiplying the p-values by the number of tests.

## 6.4. Results

GLMs showed that species, sex and site all exerted a significant effect on body size (Table 6.2). The site × sex interaction term was only significant in the case of body size, suggesting that males may increase in size to a greater extent than females at marginal populations. When differences between sites were considered, all species showed similar patterns of significantly greater size (as indicated by right forewing length) at the higher latitude site with the exception of *E. najas* females (Table 6.3, Figure 6.2). These relationships persisted after a Bonferroni correction for multiple tests.

The differences between sites in dispersal traits varied between species. In *C. splendens*, both males and females exhibited significantly higher aspect ratio at the northern site relative to the southern site (Table 6.3, Figure 6.3). In *E. najas* only the males possessed higher aspect ratio wings, with the trend in female aspect ratios becoming non-significant at the reduced α-level. Neither *P. nymphula* males nor *P. nymphula* females exhibited a significant difference in aspect ratios between the two sites at the reduced α-level.

**Table 6.2 – Results of GLM of species, sex and site as factors explaining variation in three morphological traits.**

| | Body size | WL:AL | Aspect ratio |
|---|---|---|---|
| Species | $F_{2,403}$=7579 (p<0.001) | $F_{2,402}$=1301 (p<0.001) | $F_{2,370}$=2285 (p<0.001) |
| Sex | $F_{1,403}$=545.0 (p<0.001) | $F_{1,402}$= 920.6 (p=0.007) | $F_{1,370}$=222.7 (p<0.001) |
| Site | $F_{1,370}$=173.5 (p<0.001) | $F_{1,402}$= 6.520 (p=0.011) | $F_{1,370}$=58.88 (p<0.001) |
| Sex × Site | $F_{1,370}$=9.850 (p=0.002) | $F_{1,402}$=0.560 (p=0.456) | $F_{1,370}$=2.420 (p=0.121) |

The only significant difference between sites in WL:AL was found in *C. splendens* males, where those at the margin site possess a higher WL:AL ratio (Table 6.3, Figure 6.4). In both of the expanding species the direction of the effect was similar for each trait across all species and sexes.

**Table 6.3 – Pairwise comparison of morphology at core and margin sites in three damselfly species. p-values are multiplied by 18 to control for multiple tests. [a] = right forewing length, [b] = right forewing length/abdominal length, [c] = wingspan/wing area$^2$ averaged across fore- and hindwings.**

| Trait | Species | Sex | *t* | *p* |
|---|---|---|---|---|
| Body size[a] | *C. splendens* | Male | **8.55** | **<0.001** |
| | | Female | **7.99** | **<0.001** |
| | *E. najas* | Male | **3.90** | **0.005** |
| | | Female | 2.18 | 0.594 |
| | *P. nymphula* | Male | **4.08** | **0.002** |
| | | Female | **11.96** | **<0.001** |
| WL/AL[b] | *C. splendens* | Male | **3.77** | **0.006** |
| | | Female | 1.72 | 1.602 |
| | *E. najas* | Male | 0.56 | 10.350 |
| | | Female | 1.59 | 2.124 |
| | *P. nymphula* | Male | -1.19 | 4.284 |
| | | Female | 0.89 | 6.750 |
| Aspect ratio[c] | *C. splendens* | Male | **7.69** | **<0.001** |
| | | Female | **6.44** | **<0.001** |
| | *E. najas* | Male | **3.32** | **0.036** |
| | | Female | 2.95 | 0.090 |
| | *P. nymphula* | Male | 2.40 | 0.360 |
| | | Female | -0.24 | 14.562 |

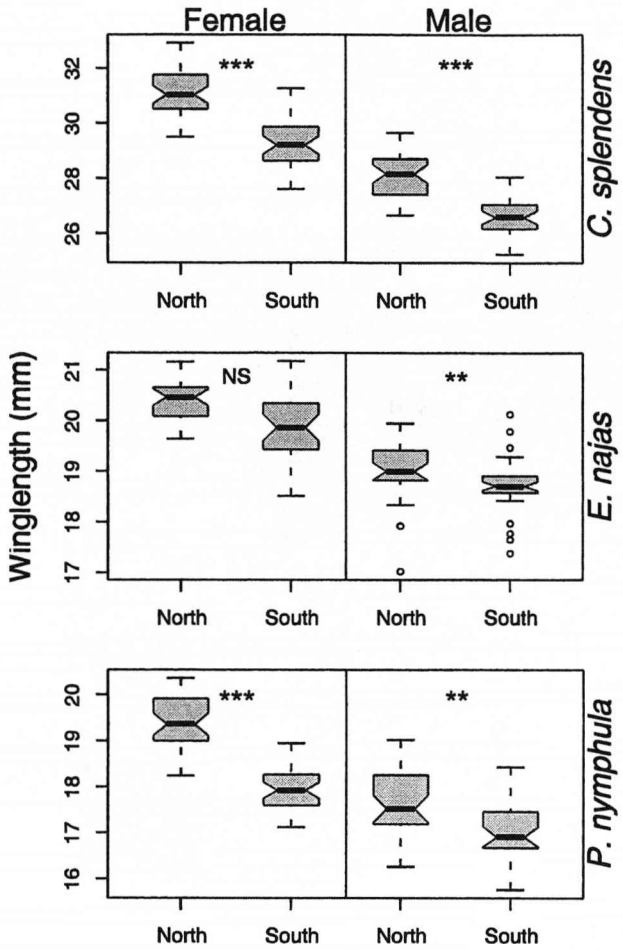


**Figure 6.2 – Variation in body size (as indicated by length of the right forewing (RFW)) between species, sexes and sites. NS=p>0.05, *=p<0.05, **=p<0.01, ***=p<0.001. p-values include Bonferroni correction for multiple tests.**

## 6.5. Discussion

### 6.5.1. Dispersal morphology

Expanding ranges are predicted to lead to the development of exaggerated dispersal traits in marginal populations. The data presented here offer some support to that hypothesis. *C. splendens*, a species which is known to have expanded its range over the past 40 years, exhibits significantly higher aspect ratio at the northern range margin relative to a population closer to the core of the range.

Higher aspect ratio reduces drag and therefore promotes dispersal over larger distances (Vogel 1981). This trait also appears to vary in male *E. najas* although to a lesser extent than in *C. splendens*. This apparent continuum of response is emphasised by additional trends which were ruled out at a

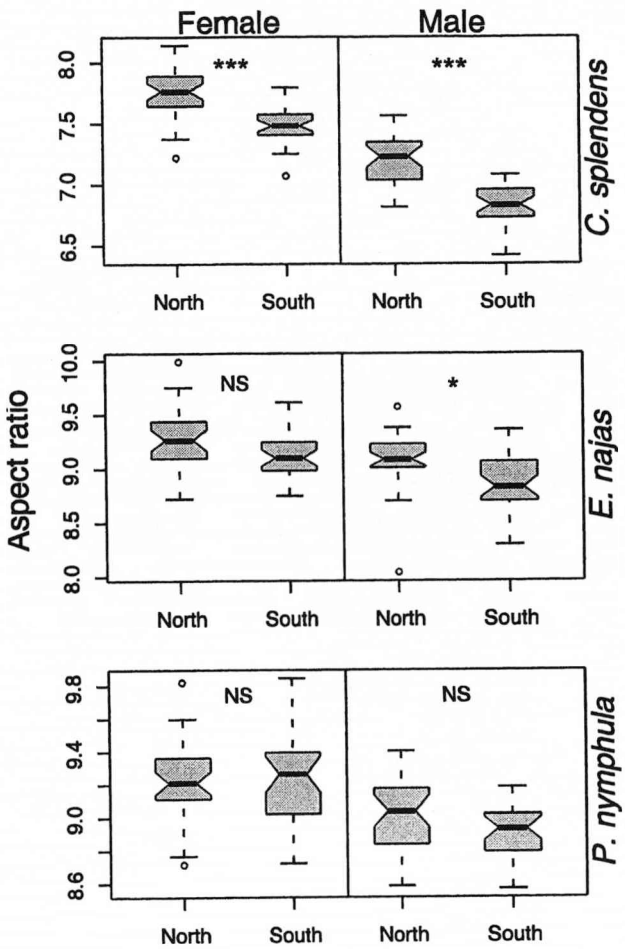


**Figure 6.3 – Variation in aspect ratio between sites for both sexes of each species. NS=p>0.05, *=p<0.05, **=p<0.01, ***=p<0.001. p-values include Bonferroni correction for multiple tests.**

reduced a-level and adds support to our ranking of species as rapidly expanding, slowly expanding and static. A similar decrease in aspect ratio in response to increasing experimental temperature has been demonstrated in *Drosophila melanogaster* (Meigen 1830) (Azevedo et al. 1998).

Results from WL:AL data also seem to support the putative ranking of the three species in order of the magnitude of selective pressure on dispersal traits. The only groups to exhibit a significant difference in WL:AL were the male *C. splendens*. In an interspecific comparison of *Calopteryx* spp., southern species were shown to exhibit a lower wing loading (Grabow and Rüppell, 1995). The same pattern of consistency in the direction of variation is present in WL:AL as in aspect ratio, with the two expanding species exhibiting higher WL:AL in the margin site but *P. nymphula* exhibiting weak and variable trends. The study by Azevedo et al. (1998) also showed that wing:thorax size

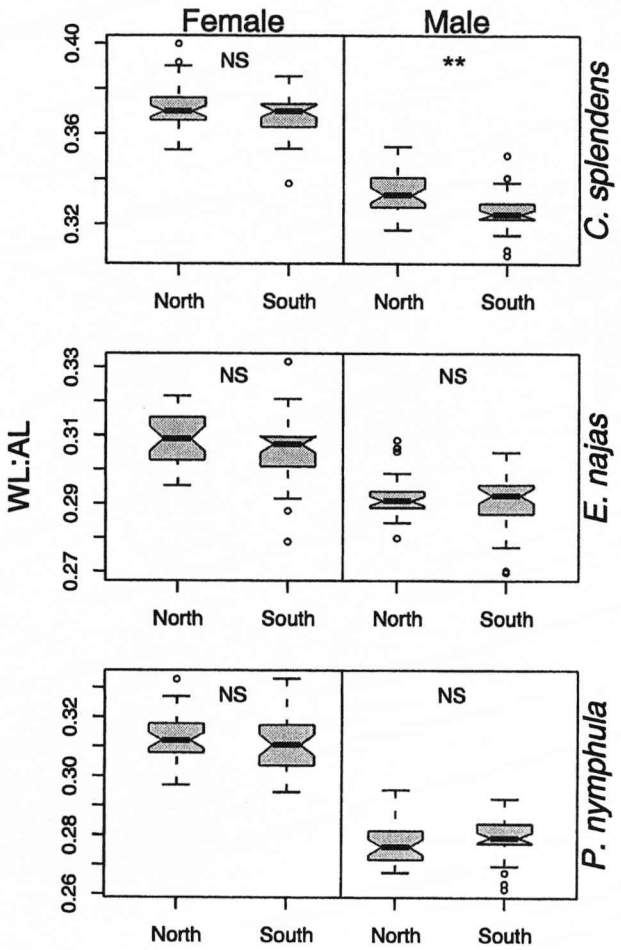


**Figure 6.4 – Variation in WL:AL (wing length : abdomen length) ratio between sites for both sexes of each species. NS=p>0.05, *=p<0.05, **=p<0.01, ***=p<0.001. p-values include Bonferroni correction for multiple tests.**

ratio (a similar measure of wing loading to our WL:AL) decreased with increasing temperature, as seen in *C. splendens* males.

There are two potential components that may contribute to the observed variation in these two dispersal traits: phenotypic plasticity and adaptation. *Drosophila melanogaster* exhibits both plasticity to temperature and adaptation along a latitudinal transect in aspect ratio and wing:thorax size ratio (Azevedo et al., 1998). However, different populations of *Drosophila subobscura* (Diptera: Drosophilidae) have been shown to vary in their degree of local adaptation in terms of wing loading (wing area/thorax length) (Gilchrist and Huey, 2004). In addition to temperature, wing morphology (length and width) in *Calopteryx maculata* was shown to vary between areas with different landscape structures (Taylor and Merriam, 1995). Although an adaptive explanation is invoked for these observations, no attempt is made to partition the effects of plasticity and genetics.

Initial colonisers at a site benefit from an *r*-selected strategy to maximise fecundity in an environment that may be exhibiting greater fluctuations than core habitats (Zera and Denno, 1997). However, increasing habitat persistence drives greater investment in reproduction, leading to benefits of a *K*-selected strategy. This mechanism may be responsible for the absence of difference between core and margin sites in *P. nymphula*. While it is not possible to rule out phenotypic plasticity to temperature, the difference in patterns of dispersal traits between *P. nymphula* and *C. splendens* suggests that the observed patterns are caused by more than simply a temperature effect.

The expansion of *E. najas* may be impaired by a close botanical association with certain floating plant species (including *Nuphar lutea* (Nymphaeaceae) (Hofmann and Mason, 2005)). This hindrance could be the reason why such morphological patterns as those seen in *C. splendens* do not occur so strongly in this species. Habitat patches with the required botanical assemblage are too poorly connected to permit sufficient dispersal to generate a selective pressure towards enhanced dispersal traits. Indeed, the opposite could be true: in a fragmented landscape there may be a pressure towards reduced dispersal if dispersal entails a high probability of mortality (Travis and Dytham, 1999).

### 6.5.2. Morphology and range expansions

Patterns of variation in body size tend to involve negative relationships with temperature and, therefore, positive correlations with increasing latitude such as those suggested by this study. However, while thermal and selective pressures may contribute to variation in body size, other factors have also been implicated in previous studies including prey density (Lawton et al., 1980) and photoperiod (De Block and Stoks, 2003). Odonata are unique in apparently exhibiting a U-shaped relationship with temperature across the entire range (Johansson, 2003), comprising a classic temperature-size pattern at the poleward range margin, relatively little variation in the core of the range and then an inverse temperature-size relationship at the equatorward range margin. However, the same study did not investigate patterns of dispersal-related traits. There is some evidence that the size of British Odonata influences their dispersal ability (Conrad et al., 1999), a pattern that is seen across a wide range of taxa (Jenkins et al., 2007). Since available habitat is likely to be both patchy and ephemeral at range margins (Brown, 1984), a greater body size in marginal populations will facilitate colonisation of this lower connectivity landscape. It might be predicted from these assumptions that the lateral component of expansion into new habitats would be slow relative to the poleward dimension.

## 6.6. Conclusions

I have demonstrated evidence for an increase in dispersal ability at range margins compared to range cores. This result supports our initial hypothesis concerning the direction of trends in wing loading and aspect ratio and conforms to results found in studies in other taxa that are expanding their ranges (Hill et al., 1999a, Phillips et al., 2006).

# *Chapter 7. Variation in wing spot size and asymmetry of the Banded Demoiselle* Calopteryx splendens

## 7.1. Abstract

Wing pigmentation of calopterygid damselflies has received considerable attention due to its role as an honest signal of male quality. I describe a quantitative analysis of this trait in two populations of the Banded Demoiselle, *Calopteryx splendens* in England. One population, sampled close to the northern limit of its range in Northumberland, exhibited substantially smaller wing spots than a population sampled in Hampshire. Wing asymmetry (in terms of length and area) did not vary between the two populations, nor did it co-vary with the size of the wing spots. I propose that the decline in wing spot size is the result of variation in climate between the two sites. Such variation in immunocompetence could contribute to the determination of range margins in this species.

## 7.2. Introduction

In most higher animals there is a dichotomy between the sexual strategies of males and those of females. Males are limited in their ability to pass on their genes by the number of females with whom they can mate. Females, on the other hand, often have access to excess mates and can concentrate on choosing which of those mates would give them the highest quality offspring. Indeed, a range of mating systems has evolved (see Corbet, 1999).

The link between odonate breeding and freshwater means that females are limited in their breeding sites. This results in territoriality in a large number of odonate species where the small number of oviposition sites is dominated by a small proportion of the total male population. What determines the outcome of these contests appears to vary between species but residency (Gribbin and Thompson, 1991), fluctuating asymmetry (Harvey and Walsh, 1993), body size (an advantage of being larger (Fincke, 1984) and smaller (Convey, 1989) have both been demonstrated) and flight morphology (De Block and Stoks, 2007) have all been implicated.

Female choice has resulted in a range of sexual ornaments which have been suggested as being arbitrarily chosen (Fisher, 1930), chosen on the basis of the traits' function as a handicap to the male (Zahavi, 1975) or chosen as a reflection of immune response to parasites (Hamilton and Zuk, 1982). The often extensive courtship displays of calopterygid dragonflies involve the use of the pigmented wings by the males. The pigment that is deposited in the wings of males during maturation (leading

to a "band" or "spot") is melanin, which is also involved in the immune response of a range of invertebrates.

Having established that variations in male wing pigmentation affected female choice (Siva-Jothy, 1999), Siva-Jothy went on to demonstrate the mechanistic link between wing pigmentation and the response to eugregarine parasites in *Calopteryx splendens xanthostoma* (Siva-Jothy, 2000). This relationship has been confirmed in subsequent studies looking at encapsulation of mite feeding tubes (Rantala et al., 2000).

Historically, *Calopteryx splendens* was restricted to the rivers of southern and central England. However, two exceptions exist in the form of clusters of populations on the Solway Firth dating back to 1936 (Clarke, 1999) and on several rivers in Northumberland (Jeffries, 2001). Populations in northeast England are relatively well connected, although low recorder effort makes this difficult to verify (Ward and Mill, 2004). On the other hand, the populations in the extreme northwest of England represent an isolated, though established, outpost. It has been suggested that further range expansion may be inhibited by the lack of suitable habitat (Ward and Mill, 2004), although habitat studies suggest that *C. splendens* is relatively catholic in its requirements (Jeffries et al., 2005).In this study I investigated the degree of wing pigmentation of two English populations of *Calopteryx splendens* sampled close to the northern limit of its range (in Northumbria) and 400km south of that (in Hampshire). The degree of pigmentation is compared between the two sites and regressions are carried out against another putative indicator of male quality, fluctuating asymmetry, which has been linked to melanotic encapsulation in previous studies (Rantala et al., 2000). Finally, an attempt is made to explain the observed variation in pigmentation in terms of climate.

## 7.3. Methods

Specimens of male *Calopteryx splendens* were collected from Finchampstead Bridge on the River Blackwater (British National Grid Reference SU775625) between 24$^{th}$ June and 28$^{th}$ June 2006 and from Bellasis Bridge on the River Blyth (NZ190776) between 4$^{th}$ July and 6$^{th}$ July 2006 (see Figure 7.1 for locations of the sites relative to the range margins of *C. splendens*). Individuals were caught using a butterfly net and placed in Ziploc bags inside a coolbox to keep them alive.

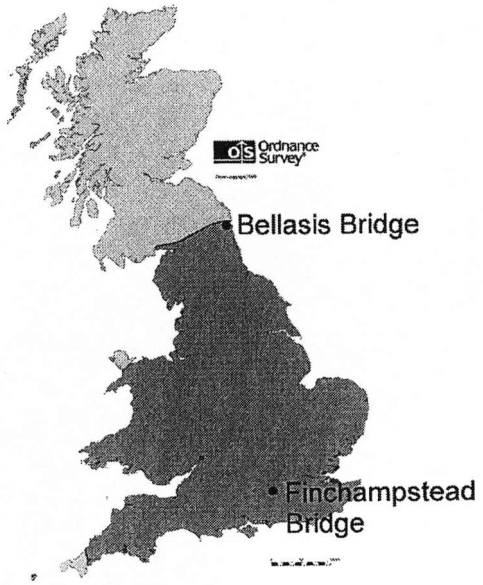


**Figure 7.1 – Map showing sampling sites for *Calopteryx splendens* in relation to the range of the species (dark grey).**

Each individual was subjected to -18°C for 150 seconds. This immobilised the animal for sufficient time to enable a digital scan to be taken of the body and wings using a Canon Canoscan LiDE 25 flatbed scanner. During scanning, animals were immobilised using microscope slides. Images were analysed using ImageJ (Rasband, 1997-2007) to find wing area.

The area of pigmentation was judged by adjusting the threshold on a greyscale image until only the pigmented region remained. The area of this region was then calculated using ImageJ. Light levels varied between scans and so the standardised methods of Siva-Jothy (1999) were not usable. The area of the pigmented region was divided by the area of the wing to give the proportion of the wing that was pigmented.

Wing length was defined as the length from the costal end of the vein separating the arculus from the discoidal cell to the tip of the wing. It was not possible to take the area of the whole wing due to interference from the body in the scan, so the wing area excluded the portion defined by the junction of the first antenodal cross-vein and the costa, the margin of the arculus and across the anal crossing to the analis (Figure 7.2). Wing length, area and wing spot measurements were all checked for repeatability by randomly choosing five individuals from each site and re-measuring all four wings (where they were undamaged). Correlations between measurements were all extremely

high: wing length, n=40, r=0.999, p<0.001; wing area, n=39, r=0.998, p<0.001; wing spot, n=39, r=0.974, p<0.001.

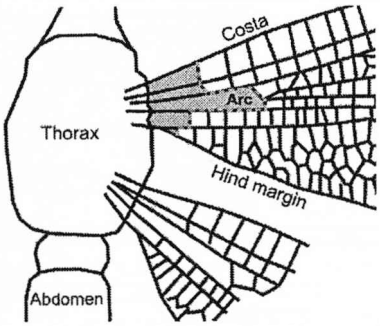


**Figure 7.2 – The shaded area indicates the proximal portion of the wing excluded from measurement of wing area (see text for details). Arc = arculus.**

Wing fluctuating asymmetry (FA) was calculated for both wing area and wing length. Differences between left and right wings for both fore- and hindwings were determined. Each was divided by the mean value for that trait to give a FA value standardised against body size. Each pair of wings was then averaged to give a mean wing area FA and a mean wing length FA.

The two populations were compared to test for differences in the proportion of the wing that was pigmented, mean wing area FA and mean wing length FA using two-sample, two-tailed t-tests. An analysis of covariance (ANCOVA) was employed with FA as the response, site as a factor and the proportion of pigmentation as a covariate to test for a correlation between these two measures (FA and size of pigment spot) of male quality.

Climate data were extracted from two Meteorological Office weather stations for the period 1 June – 31 July 2006. These weather stations were "Reading University: Whiteknights" (source identification 830, 11km northwest of Finchampstead Bridge) and "Wallington" (source identification 300, 16km northwest of Bellasis Bridge). A paired t-test was used to test for difference between the two time-series.

## 7.4. Results

The proportion of the wing that was pigmented was significantly lower in the northern population from Bellasis Bridge compared to the southern population from Finchampstead Bridge ($t=-8.87$, $p<0.001$). Mean proportion of wing area pigmented was 0.435 ± 0.011 (S.E.) in the northern population compared to 0.545 ± 0.006 in the southern population (Figure 7.3 and Figure 7.4).

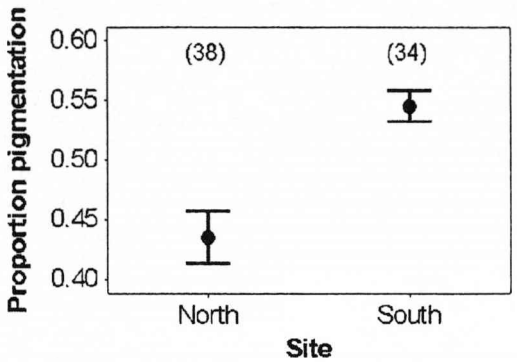


**Figure 7.3 – Mean proportion of the wing that was pigmented in specimens of *Calopteryx splendens* caught at Finchampstead Bridge and Bellasis Bridge. Numbers in brackets are sample sizes and error bars are 95% confidence intervals.**

There was no difference between sites for either wing area FA ($t=1.11$, $p=0.272$) or wing length FA ($t=0.86$, $p=0.395$). Furthermore, there was no significant relationship between wing area FA (site: $F=71.02$, $p<0.001$; wing area FA: $F=1.38$, $p=0.244$) or wing length FA (site: $F=74.92$, $p<0.001$; wing length FA: $F=1.79$, $p=0.186$) with the proportion of the wing that was pigmented. The same was true when absolute wing spot size was used instead of the proportion of the wing that was pigmented.

An analysis of the climate data showed that the mean temperature at Finchampstead Bridge was 19.03°C ± 0.44 compared to 15.30°C ± 0.38 at Bellasis Bridge, an average difference of 3.73°C. This difference was statistically significant (paired t-test, $t=14.33$, $p<0.001$, Figure 7.5).

## 7.5. Discussion

I am not aware of such an inter-population difference in wing spot size having been demonstrated previously. Other analyses have focused on within-population variation to investigate patterns of reproductive behaviour.

I have good reason to suspect that the difference in ambient temperature between the two sites has influenced the development of this trait. First, haemocyte (melanotic cells in the haemolymph)

concentrations are higher at higher temperatures in butterflies (Pandey et al., 2007). Thus there may be a larger circulating pool of melanin in the haemolymph to be deposited in the wings during maturation at the southern site. Second, atmospheric temperatures are likely to play the main role in the development of this trait as wing pigmentation develops entirely after emergence from the water. Odonate larvae can use microclimates within water bodies to lessen the impacts of environmental temperature variation (Sternberg, 1997). Finally, higher temperatures have been shown to increase melanotic encapsulation of the feeding tubes of ectoparasitic mites in *Lestes forcipatus* (Robb and Forbes, 2005).

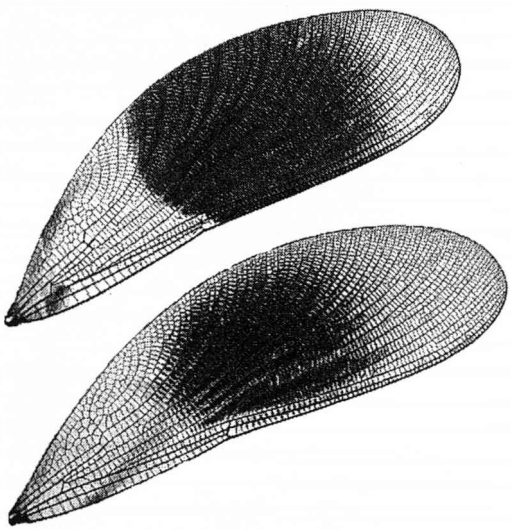

**Figure 7.4 – Illustration of variation in wing spot size in *Calopteryx splendens* specimens from Hampshire (above), proportion of wing pigmented = 0.525 and Northumbria (below), proportion of wing pigmented = 0.339.**

Previous analyses have shown that absolute fluctuating asymmetry (FA) of wing spot area correlates with the rate of melanotic encapsulation of mite feeding tubes in *Calopteryx splendens* (Rantala et al., 2000). This physiological phenomenon involves the envelopment of foreign objects (such as pathogens or parasites) by melanised cells in the haemolymph and forms the basis of the invertebrate immune response. The absence of a relationship between wing FA and wingspot size in the present study is surprising given the vital role that *C. splendens* wings play in courtship behaviour, the pigmented spot being of particular significance. However, the ability of studies such as this to detect FA has been questioned in the past on the grounds that the magnitude of any effect is small relative to measurement error and that traits vary in their susceptibility to FA.

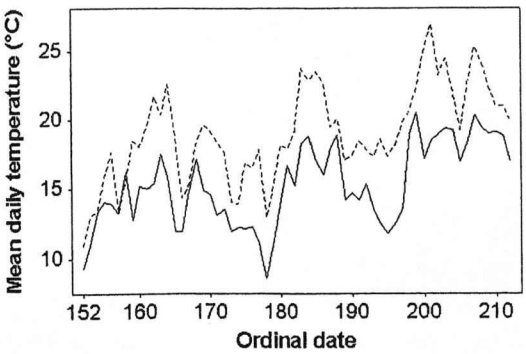


**Figure 7.5 – Variation in mean daily temperature between Finchampstead Bridge (dotted line) and Bellasis Bridge (solid line). Ordinal date is days since 1st January, so 152 is 1st June.**

A recent study has shown that wing shape deviates from normal in populations of *Coenagrion puella* close to its northern limit near Forfar, Scotland (Hassall et al., 2008). The authors suggested that this deviation may contribute to the maintenance of its northern range margin due to the way in which progressively more-deformed wings hinder flight closer to the margin. In the same way, a decline in immunocompetence closer to the northern range margin in *C. splendens* could serve to increase mortality, thereby contributing to the processes that limit its northern distribution. Another possibility is that an energetic trade-off is taking place between the maintenance of dispersal-related traits and investment in immune function.

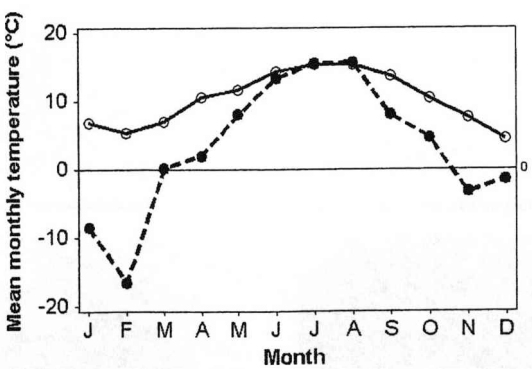


**Figure 7.6 – Mean monthly temperature variation during 2007 at Leeming, England (54.3°N, 1.5°W), open circles, solid line and Kajaani, Finland (64.3°N, 27.7°E), closed circles, dashed line. Data available from http://data.giss.nasa.gov/gistemp/station_data/**

The variation in the latitude of the range margin between Britain (c. 55°N) and continental Europe (c. 64°N in Finland) highlights some aspects of regional climate that are important to *C. splendens*. The Scandinavian populations experience extremely cold winters against which larvae are largely protected by the buffering effects of their lotic, aquatic environment. However, when this environment is left after emergence during the summer, temperatures are comparable between the two regions (Figure 7.6). Furthermore, the longer day lengths during summer at higher latitudes increase the amount of solar radiation that the damselflies can make use of through basking. It may be that summer temperatures are the limiting factor in the distribution of *C. splendens* and such a limitation may be tied to some aspect of adult physiology such as the immune response suggested here.

# *Chapter 8. Latitudinal variation in morphology in two sympatric damselfly species with contrasting range dynamics*

## 8.1. Abstract

Geographic range expansion is one of the best documented macroecological consequences of climate change. A concomitant change in morphology has been demonstrated in some species. The relationship between latitudinal variation in morphology (e.g. Bergmann's rule) and the morphological consequences of microevolutionary pressures at expanding range margins have received little attention in the literature. Here I compare morphology of males of two Palaearctic damselfly species, *Coenagrion puella* and *Pyrrhosoma nymphula*. *C. puella* has recently expanded its range from the north of England into Scotland. *P. nymphula* does not exhibit a range margin in the United Kingdom and has established populations in northern Scotland. I demonstrate evidence for spatially correlated variation in body size across the sampling sites between the two species but a deviation in patterns of dispersal-related morphology. *P. nymphula* exhibited very weak relationships between dispersal-related morphology (wing loading and thorax : abdomen mass ratio) and latitude. However, the more southerly-distributed *C. puella* exhibited strong relationships between mass investment in dispersal-related morphology and latitude. These trends appear to indicate compensatory growth patterns in cooler environments like those demonstrated for other species. The limits of this compensation for conditions that are close to the limits of a species' tolerance may contribute to the determination of the range margin. Greater variation in morphology towards the range margin has been observed in previous studies in Odonata. As such, the location of the sampling sites relative to the range margin of each species (closer in *C. puella* than *P. nymphula*) is highlighted as a potential contributing factor to the variation observed.

## 8.2. Introduction

There is little doubt now that, for whatever reason, the global climate is rapidly warming (Jones et al., 2001). This rapid climate change has resulted in a number of impacts on the earth's biota which have been well-documented (Parmesan and Yohe, 2003, Walther et al., 2005). One of the best described responses to this environmental change has manifested as a poleward shift in the geographic distributions of a range of taxa (Hickling et al., 2006, Parmesan et al., 1999).

Such variation in geographic ranges occurs through the dynamic processes of extinction and colonisation at range margins. Colonisation of new habitats at the range margin is achieved by a non-representative sample of the founding population, i.e. by those individuals that exhibit traits

that confer an advantage in dispersal. Theoretically, therefore, there should be both a genetic (Hill et al., 2006) and phenotypic (Thomas et al., 2001, Phillips et al., 2006) footprint of range expansion detectable in those species that are responding to climate change.

However, the detection of a phenotypic footprint is complicated by the additional effects of latitude on morphology. This includes one of the first ecological rules formulated by Bergmann (1847) which stated that body size increased and limb length decreased with latitude. This rule has recently enjoyed a resurgence as the temperature-size rule (Atkinson, 1994). However, despite extensive recent study, there has been little success in elucidating the mechanisms behind this phenomenon (Angilletta Jnr. and Dunham, 2003, Walters and Hassall, 2006).

Teasing apart the contribution that genetics makes to the phenotypic pattern has been accomplished using common garden experiments (Hill et al., 1999a) and molecular techniques (Hill et al., 2006) in the speckled wood butterfly, *Pararge aegeria* (Lepidoptera: Nymphalidae). However, the majority of range expansions occur along a north-south axis making it difficult to tease apart the effects of an expanding range and varying latitude.

The order Odonata has persisted through previous, rapid climatic shifts during the Quaternary Period (Adams et al., 1999). This suggests that the order should possess traits which will aid in future encounters with similar environmental change, such as that which is currently occurring (Balmford, 1996). Indeed, poleward range expansions have been documented in a range of European species (Hickling et al., 2006, Ott, 2001). The observation of contemporary range shifts is not surprising given the apparent constancy of other insect groups in the face of quaternary climate fluctuations (Coope, 1978).

Odonate morphology has been studied in a range of contexts, including dispersal (Conrad et al., 2002, Anholt, 1990), landscape structure (Taylor and Merriam, 1995), predator defences (Johansson and Samuelsson, 1994), phylogenetics (O'Grady and May, 2003) and latitude-size relationships (Johansson, 2003), as well as range expansion (Hassall et al., 2008). Johansson (2003) detected variation in body size across the latitudinal range in *Enallagma cyathigerum*, which highlights the importance of considering this aspect of morphology at the range margin.

I describe a comparative study of two common species of Palaearctic Odonata with overlapping distributions but which differ in their range dynamics. I demonstrate that a species that is not

expanding its range (*Pyrrhosoma nymphula*) exhibits little or no relationship between latitude and body size and flight morphology. However, a species that is expanding its range (*Coenagrion puella*) exhibits strong relationships with latitude in these traits. The direction of trends in *C. puella* appears to correspond to a compensation for declining muscular efficiency at lower temperatures close to the range margin.

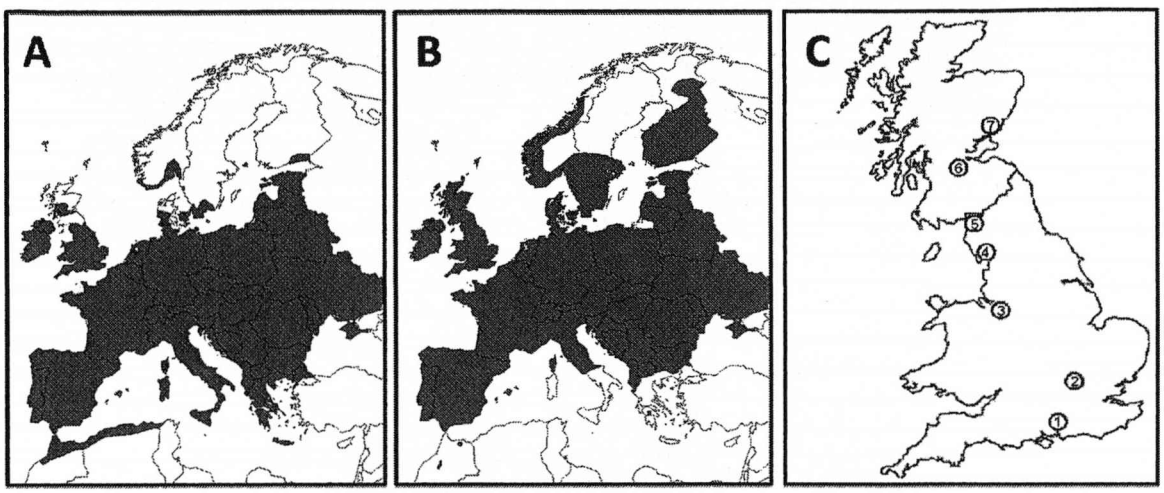


**Figure 8.1 – Maps reproduced from Askew (2004) illustrating European ranges for (A) *Coenagrion puella* and (B) *Pyrrhosoma nymphula* and (C) the UK sampling localities for both species. Locality numbers in (C) relate to locality numbers in Table 8.1.**

## 8.3. Methods

### 8.3.1. Study species

*Coenagrion puella* is a coenagrionid damselfly which is distributed throughout Europe (Figure 8.1). However, this species is only found in southern Scotland and is only found around the southern coast of Scandinavia. As such, it can be assumed that this species has the potential to expand its range into the north of the UK.

*Pyrrhosoma nymphula* is a coenagrionid damselfly which is also distributed throughout Europe including considerable areas of Scandinavia and northern Russia (Figure 8.1). Importantly, it has been recorded on or near the northern coast of Scotland since 1910 (Orkney Mainland, 58.97N - 3.39E), suggesting that the species has long since filled available habitats within the UK.

**Table 8.1 – Summary of sampling sites for two species of damselfly in the UK.**

| | *Coenagrion puella* | | | *Pyrrhosoma nymphula* | | |
|---|---|---|---|---|---|---|
| Locality | Site | Latitude | Longitude | Site | Latitude | Longitude |
| 1 | QECP | 50.961 | -0.978 | QECP | 50.961 | -0.978 |
| 2 | Coronation Pit | 52.083 | -0.495 | Titchmarsh NR | 52.414 | -0.521 |
| | Felmersham GP | 52.215 | -0.551 | | | |
| 3 | Vale Royal | 53.230 | -2.541 | Abbots Moss | 53.214 | -2.609 |
| 4 | Duddon Mosses | 54.258 | -3.199 | Duddon Mosses | 54.258 | -3.199 |
| 5 | Drumburgh Moss | 54.919 | -3.159 | Bowness Common | 54.928 | -3.207 |
| 6 | Tailend Moss | 55.893 | -3.591 | Tailend Moss | 55.893 | -3.591 |
| 7 | Loch of Kinnordy | 56.676 | -3.047 | Dykehead pond | 56.730 | -3.023 |

## 8.3.2. Sampling and measurement

Sampling localities were selected to provide a latitudinal transect 640km in length through the United Kingdom (Table 8.1 and Figure 8.1). Both species were sampled at each locality either within the same site where possible (three localities), or else at nearby pairs of sites (four localities). Note that *C. puella* was sampled at two different sites within locality 2 to provide a comparison within a locality.

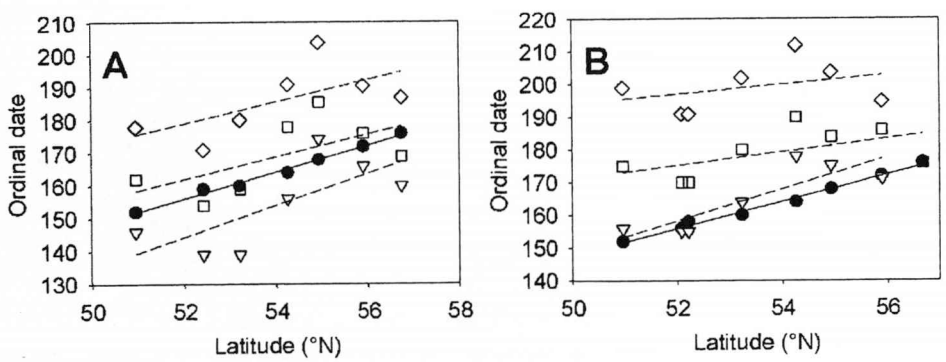


**Figure 8.2 – Variation in flight period with latitude in (A) *Pyrrhosoma nymphula* and (B) *Coenagrion puella*. Dotted regression lines show Q1 (open triangles), Q2 (open squares) and Q3 (open diamonds) flight dates. Dates at which sites were sampled are shown by closed circles and a solid regression line. Phenology data are from 1995-2005.**

Odonate body size has been shown to decline with time of season (Banks and Thompson, 1985a) and so care was taken to sample each site at the same time of season. To accomplish this, the

British Dragonfly Society's extensive database of sightings was used to plot latitudinal variation in flight periods and sampling dates were specified accordingly (Figure 8.2).

At least 30 males of each species were caught by the water body with a butterfly net and immediately preserved in ethanol for later processing. These specimens were then dissected and all four wings were preserved between pieces of adhesive tape. These were then scanned using a flatbed scanner and ImageJ (Rasband, 1997-2007) was used to make measurements of wing length and wing area on the resulting images.

Due to difficulties with defining the proximal portion of the wing around the wing plug, the area and length measurements only included the portion of the wing that lay distal to the first cross vein (Figure 8.3). Repeated measurements from 35 randomly selected specimens were highly significantly correlated with first measurements (right forewing length, $r=0.996$, $p<0.001$; right forewing area, $r=0.995$, $p<0.001$). The abdomen and thorax were dried at 60°C for 24 hours and then weighed.

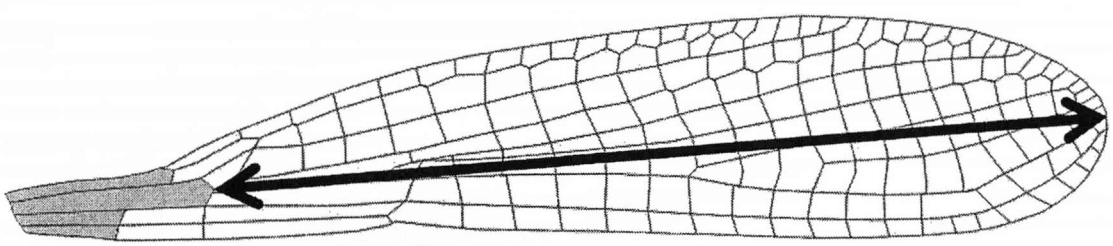

**Figure 8.3 – Diagram of wing of *Coenagrion puella* showing wing length measurement (double-headed arrow) and region excluded from area measurement (shaded in grey). See text for details.**

### 8.3.3. Data analysis

Aspect ratio of the wings was calculated for both hind- and forewings as wingspan$^2$/wing area and then used to calculate a mean aspect ratio for each individual. Wing loading was calculated as (thoracic mass + abdominal mass)/wing area, where wing area included all four wings. The ratio of thoracic and abdominal mass (hereafter "T:A ratio") was calculated by simply dividing the thoracic mass by the abdominal mass. Body mass was simply the sum of thoracic and abdominal mass and the right forewing was used as the representative wing length.

In order to investigate relative variations in the size of the measured traits, data were standardised to between zero and one. Means of each trait at each site were taken to eliminate the potential effects of pseudoreplication. To test for a difference between species, an ANCOVA was used to analyse each of the variables (wing length, body mass, wing loading, T:A ratio and aspect ratio) with latitude as a covariate and species as a factor. For each species individually, linear regressions were used to test for effects of latitude on each of the variables. Equality of variance across sites was tested for in the wing length data using Bartlett's test as the data were normally distributed.

## 8.4. Results

*P. nymphula* and *C. puella* differed significantly in size when all specimens were pooled (two-sample two-tailed t-test, wing length: $t=14.13$, $p<0.001$; body mass: $t=23.09$, $p<0.001$). *P. nymphula* males possessed wings that measured on average 18.9mm ± 0.051 (mean ± SE) compared to those of *C. puella* males that measured 17.9mm ± 0.047. *P. nymphula* body mass was 8.33mg ± 0.084 compared to *C. puella* which weighed 5.99mg ± 0.057.

**Table 8.2 – Results of ANCOVAs investigating variations in four dispersal-related traits between species (*C. puella* and *P. nymphula*, as a factor) and with latitude (as a covariate).**

| | Species | | Latitude | |
|---|---|---|---|---|
| **Trait** | **F** | **p** | **F** | **P** |
| Wing length | 0.08 | 0.785 | 4.63 | 0.053 |
| Body mass | 2.90 | 0.114 | 8.89 | 0.011 |
| Wing loading | 23.99 | <0.001 | 1.39 | 0.262 |
| T:A ratio | 12.67 | 0.004 | 8.60 | 0.013 |
| Aspect ratio | 456.18 | <0.001 | 1.09 | 0.318 |

Body mass and wing length increased with latitude in both *C. puella* and *P. nymphula* (Table 8.2, Figure 8.4A and B), although this was not significant in the case of wing length. There was a significant species effect on the three dispersal traits (wing loading, T:A ratio and aspect ratio), as well as a significant effect of latitude on T:A ratio (Table 8.2).

*P. nymphula* exhibited no significant correlations between any of the traits measured and latitude (Table 8.3). This is in contrast to the results for *C. puella*, which exhibited significant correlations with three traits (body mass, wing loading and T:A ratio, Table 8.3, Figure 8.4). Positive correlations

were found between latitude and T:A ratio and body mass in *C. puella* whereas a negative correlation was found between latitude and wing loading. It is worth noting that these three traits were those which involved mass measurements. The two traits relating solely to wing measurements (wing length and aspect ratio) did not vary significantly with latitude, although wing length approached significance (p=0.079).

**Table 8.3 – Correlations between dispersal-related traits and latitude in two species of damselfly. Significant correlations are highlighted in bold.**

| | *C. puella* (n=8) | | *P. nymphula* (n=7) | |
|---|---|---|---|---|
| **Trait** | **r** | **P** | **r** | **P** |
| Wing length | 0.653 | 0.079 | 0.340 | 0.455 |
| Body mass | **0.808** | **0.015** | 0.408 | 0.364 |
| Wing loading | **-0.775** | **0.024** | 0.377 | 0.405 |
| T:A ratio | **0.902** | **0.002** | 0.105 | 0.823 |
| Aspect ratio | 0.397 | 0.330 | 0.284 | 0.538 |

Bartlett's test showed that there was no significant difference in variance across the latitudinal transect in *P. nymphula* ($X^2$=6.92, p=0.328; Figure 8.5). However, there was a significant difference in variance in *C. puella* ($X^2$=22.4, p=0.002; Figure 8.5). This variation in *C. puella* appears to involve a contraction of variance with increasing latitude in the four southern sites (Figure 8.5). The fifth site then reverts to a variance similar to that of the first site followed by a renewed trend towards declining variance.

## 8.5. Discussion

*P. nymphula*, a species that has been established throughout the UK for at least a century, exhibited no significant trends with latitude in any of two size measurements (body mass and wing length) or three dispersal-related traits (wing loading, T:A ratio and aspect ratio). However, *C. puella*, a species that is known to be expanding its range into mid-Scotland, exhibited significant latitudinal relationships with body mass, wing loading and T:A ratio. Body mass and wing length both increased with increasing latitudes, in line with expectations from the temperature-size rule. Variation in wing loading and T:A ratio appears to follow the pattern that would be expected if these two traits were compensating for decreased flight muscle efficiency at lower temperatures. Both of these traits have been associated with flight acceleration in Lepidoptera (Berwaerts et al., 2002).

T:A ratio could potentially reflect the relative apportioning of investment between reproduction (abdomen) and dispersal (thorax) in females and has been linked to colonisation ability in Lepidoptera (Hill et al., 1999a). However, latitude-size relationships would mean that males would be predicted to exhibit the same pattern, to increase the mass of flight muscle relative to the rest of the body. Thoracic mass correlates with the amount of energy produced per wing stroke in Anisoptera (May, 1981).

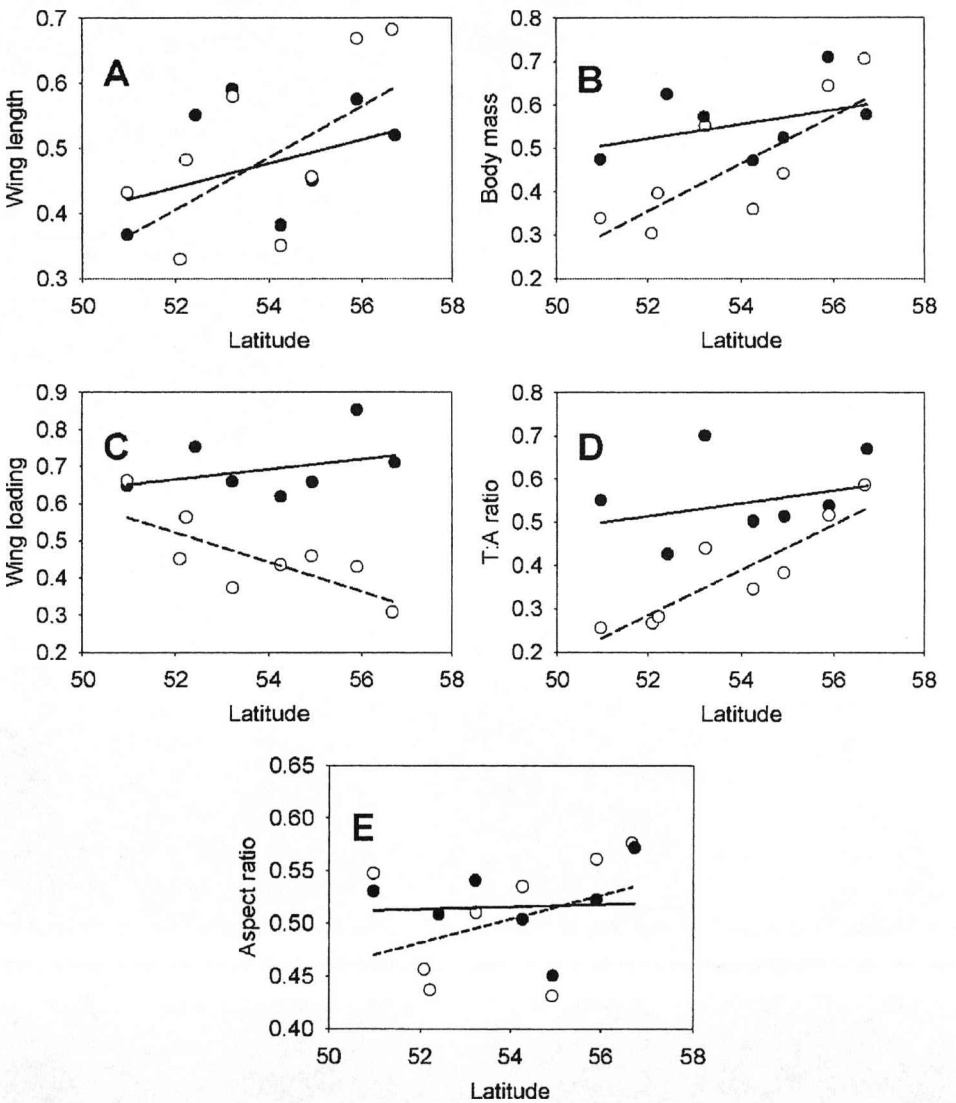


**Figure 8.4 – Mean values of (A) wing length, (B) body mass, (C) wing loading, (D) T:A ratio and (E) aspect ratio for *Coenagrion puella* (open circles, dotted lines) and *Pyrrhosoma nymphula* (closed circle, solid lines) at each site plotted against the latitude of that site. Lines are linear regressions (see Table 8.3 for statistics).**

The decline in wing loading is particularly significant, since an increase in size (along all linear dimensions) would be expected to produce an increase in the amount of mass (proportional to volume, length$^3$) per unit area of wing (length$^2$). Wing loading has been shown to be positively associated with latitude in European *Drosophila subobscura* (Diptera: Drosophilidae) (Gilchrist and Huey, 2004), as has wing aspect ratio in *Drosophila melanogaster* (Diptera: Drosophilidae) (Azevedo et al., 1998).

Studies across the entire latitudinal range of *Enallagma cyathigerum* suggested a U-shaped relationship between body size and latitude (Johansson, 2003). It may be that the location of the sampled latitudinal transect relative to the range margins of each species has determined the extent of variation in size that was detected. In the present study *P. nymphula* was sampled closer to the central depression of the U-shape, whereas *C. puella* was sampled at the extreme of an ascending limb. However, it is important to note that there is a range of other factors that have also been shown to influence odonate body size, including prey density (Lawton et al., 1980), seasonal time constraints (De Block and Stoks, 2003, Johansson and Rowe, 1999) and predation (Blumenshine et al., 2000).

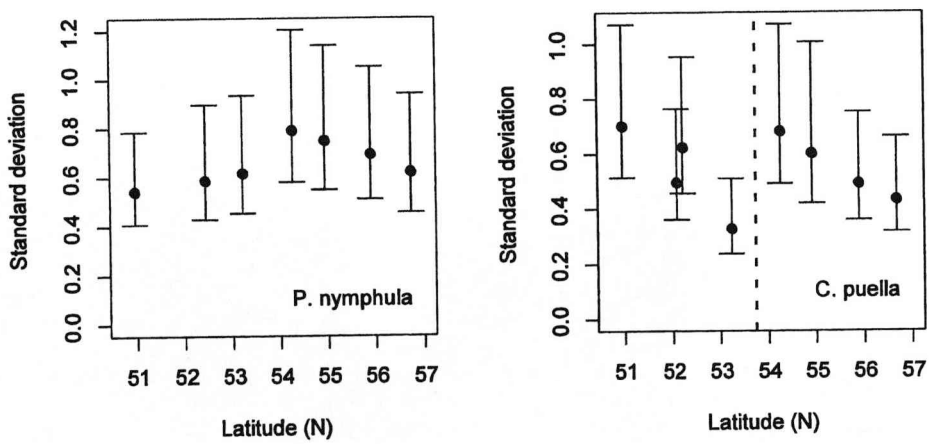


**Figure 8.5 – Trends in standard deviation in right forewing length across a latitudinal gradient in (left) male *Pyrrhosoma nymphula* and (right) male *Coenagrion puella*. Bars are 95% CI. Dashed, vertical line in the right-hand plot represents division of populations into two putative voltinism categories.**

The patterns of variance in the body size measurements for *C. puella* may be indicative of a shift in voltinism generated by seasonal time constraints. Such a pattern of variance has not been reported

before, although it may be present in data from other studies (e.g., Johansson, 2003). Such a pattern in declining body size variance could result from increasing physiological pressure from photoperiod to accelerate growth with decreasing length of growth season. Of the range of growth rates that are possible within a population, a proportion of the lowest which would not have made the winter critical size (Norling, 1984b) are accelerated, thus reducing the variance.

The latitude of the voltinism shift predicted from the present data on *C. puella* (between 53.23 and 54.26°N, marked approximately by the dotted vertical line in Figure 8.5) concurs with the field studies which show univoltinism between 41.73 and 48.27°N with a "split cohort" (both uni- and semivoltinism) recorded at 53.47°N (see appendix in Corbet et al., 2006) and at three ponds between 53.00°N and 53.35°N (Banks, 1985). It would be assumed that any population north of this point would be purely semivoltine, although none has been recorded. It is reasonable to assume that climate change has resulted in a poleward shift in voltinism thresholds over the time since Banks' data were collected.

By way of contrast, *P. nymphula* is generally considered to be uniformly semivoltine across its British range, with some northern populations taking three years per generation at high densities (Macan, 1964, 1974). Univoltinism has been recorded at 47°N and semivoltinism recorded between 50.82°N and 56.73°N (Dykehead pond) (again, see Corbet et al., 2006 for details). However, no new studies have been carried out in southern England since 1993.

## 8.6. Conclusions

Damselflies vary in the relationship between latitude and morphology. This result may be due to the location of sampling sites relative to each of the species' ranges. The data support a variation in the gradient of the latitude-size relationship which is in agreement with those trends detected in previous studies (Johansson, 2003). *C. puella*, the species sampled at its range margin, showed strong latitudinal variation in mass and three dispersal traits with the direction of variation suggesting a trend towards compensation for decreased flight muscle efficiency at higher latitudes (lower temperatures). Also in this species, evidence was found for an effect of growth season and photoperiod on body size distributions suggesting a progressive homogenisation of development rates at increasing time stress.

# *Chapter 9. Wings of* Coenagrion puella *vary in shape at the northern range margin*

## 9.1. Abstract

A previous study has shown that wing size in *Coenagrion puella* varied considerably along a latitudinal gradient in the UK. Using landmark data from wing images, patterns of shape variation were also determined along the same transect by geometric morphometric analysis of wing shape. Wing shape was uniform at all sites other than those closest to the range margin, which differed significantly. The potential mechanisms that might have generated such between-population variation are discussed.

## 9.2. Introduction

It has always been assumed that odonate wing venation varies relatively little between individuals of the same species and this assumption has formed the basis for studies of phylogeny within this taxon (Trueman, 1996). However, damselflies and dragonflies have been shown to vary in body size with latitude (for a review see Corbet, 1999 p.624) and a component of this is likely to be manifested in wing size.

During sampling of *Coenagrion puella* for a study on variation in body size with latitude, it was noted that there was substantial variation in wing length (Hassall and Thompson, 2008). The aim of the present study was to ascertain which area of the wing was undergoing the size change. Geometric morphometrics is a field which has been greatly facilitated by the increase in computing power over the past few decades (Richtsmeier et al., 2002). This technique makes use of *x,y* coordinates ("landmarks") to quantify shape and allows both a comparison of shape between objects and an investigation into which landmarks cause the variation. Geometric morphometrics has been used to distinguish between species and sexes of Hymenoptera (Pretorius, 2005) through the analysis of multivariate, landmark data.

## 9.3. Methods

During the summer of 2007, at least 30 male adult *Coenagrion puella* were removed from each of a series of eight sites across Britain (Table 9.2) to investigate variation in morphometry. The sampling sites are shown in Figure 9.1 in the context of the British (main) and European (inset) ranges. These individuals were scanned using a flatbed scanner and measured using the ImageJ analysis tool (Rasband, 1997-2007). To look at changes in shape of wings, the tpsDIG2 computer program

(available from http://life.bio.sunysb.edu/morph/) was used to digitise 14 out of roughly 220 nodes as landmarks on the right fore wing (or left when the right was missing or damaged) of all *C. puella* specimens that possessed at least one intact fore wing (Figure 9.2, Table 9.2). Those specimens not possessing at least one intact forewing were excluded, resulting in reduced sample sizes. These landmarks were considered to represent the major dimensions of the wing.

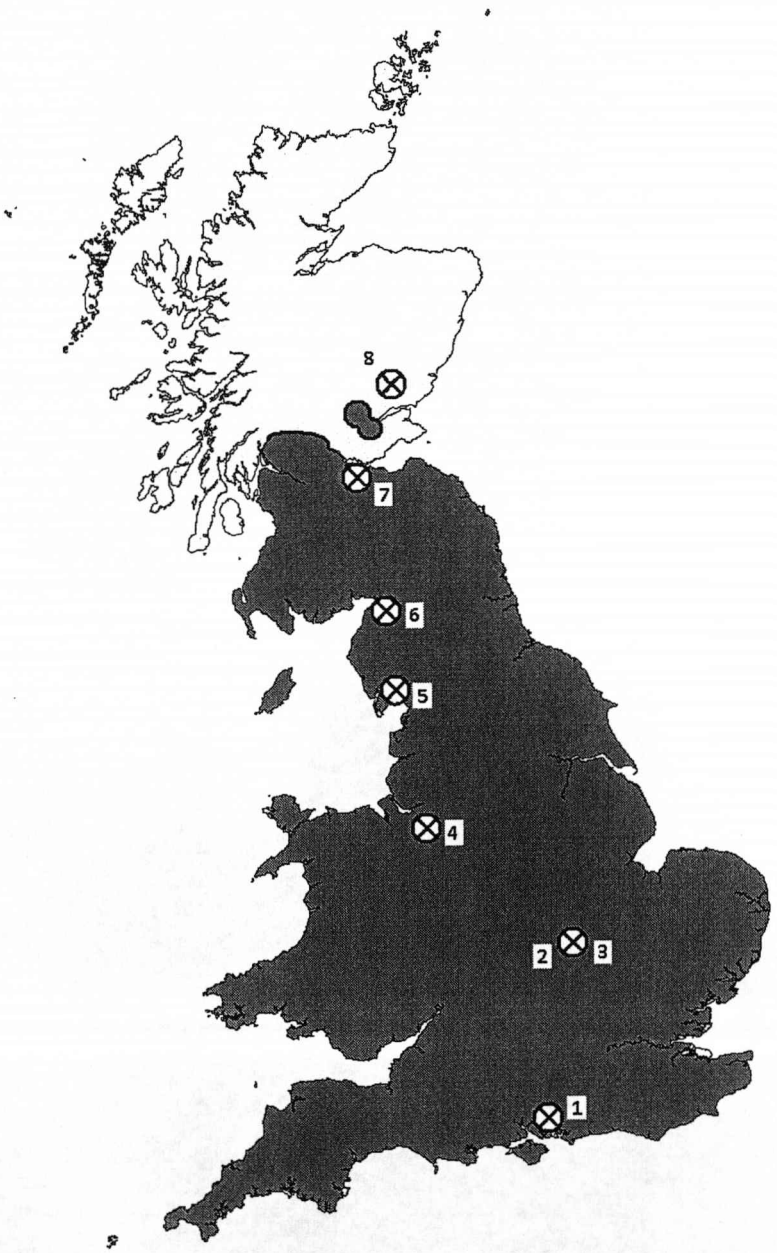


**Figure 9.1 – The distribution of *Coenagrion puella* in Britain (dark grey). Sampling sites are marked with "⊗" and numbers correspond to site numbers in Table 9.1.**

**Table 9.1 – Locations of sites comprising a latitudinal gradient of the UK and sample sizes (*n*) of male *Coenagrion puella* with intact forewings collected from each site.**

| Site number | Name | Long | Lat | *n* |
|---|---|---|---|---|
| 1 | Queen Elizabeth Country Park | -0.978 | 50.961 | 29 |
| 2 | Coronation Pit | -0.495 | 52.083 | 30 |
| 3 | Felmersham Nature Reserve | -0.551 | 52.215 | 29 |
| 4 | Vale Royal Locks | -2.541 | 53.23 | 25 |
| 5 | Duddon Mosses | -3.199 | 54.258 | 28 |
| 6 | Drumburgh Moss | -3.159 | 54.919 | 22 |
| 7 | Tailend Moss | -3.591 | 55.893 | 30 |
| 8 | Loch of Kinnordy | -3.047 | 56.676 | 30 |

Landmarks taken from wing scans were analysed using the PAST software package (available from http://folk.uio.no/ohammer/past/). First, landmarks were Procrustes transformed to standardise the locations. This method of standardisation removes variation in scaling and rotation but preserves shape. A MANOVA test was then used to examine differences between sites in shape and a post-hoc pairwise comparison of sites was performed using Hotelling's $T^2$ test.

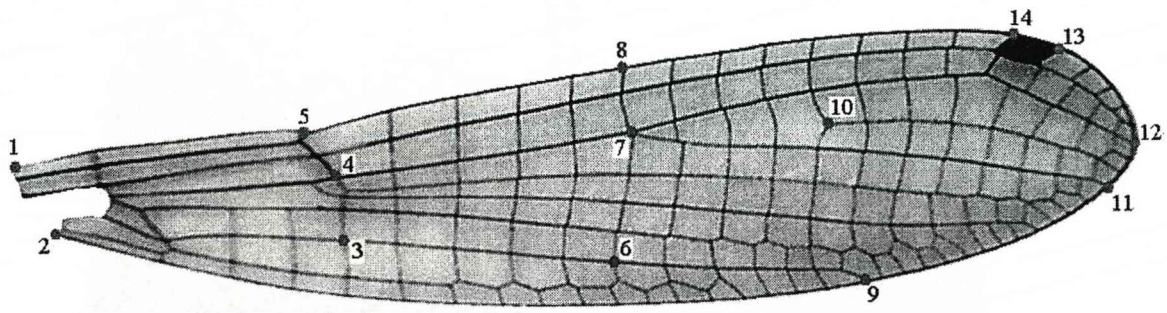


**Figure 9.2 – The 14 landmarks digitised from the *Coenagrion puella* wing scans — 1: 1st junction of costa; 2: junction of analis and anal crossing; 3: nodal junction of costa; 4: sub-nodus; 5: nodus; 6: junction of cubitus and 5th post-nodal cross vein; 7: split of 2nd and 3rd branch of radius; 8: junction of costa and 5th post-nodal cross vein; 9: termination of cubitus; 10: beginning of 2nd intercalary radial vein; 11: termination of 3rd radial vein; 12: termination of 2nd radial vein; 13: distal, exterior corner of pterostigma; 14: proximal, exterior corner of pterostigma.**

## 9.4. Results

The variation in the location of transformed wing landmarks is plotted in Figure 9.3. A qualitative analysis of this image suggested that there was relatively little pre-nodal variation in size or shape judging by the small clusters of points around landmarks 1-5. The greatest variation occurred in the central portion of the wing, with elongated clouds of points around landmarks 6-10. There was little variation in landmarks 11-14. From this cursory glance, it appeared that the majority of the size variation was generated by a general elongation of the post-nodal section of the wing.

This was supported by a comparison of the mean conformations of landmarks from the two sites exhibiting the greatest divergence in size (Coronation Pit as the smallest and Loch of Kinnordy as the largest; Figure 9.4). Again, landmarks 1-5 and 11-14 exhibited little variation between the two sites. However, landmarks 6-8 were closer to the proximal portion of the wing in the population from Coronation Pit. This suggested that the variation in size may be due to an elongation of this region of the wing in the population from Loch of Kinnordy.

**Table 9.2 – Pairwise comparison of wing shape in *Coenagrion puella* at eight sites along a latitudinal transect in the UK. Values are p-values arising from Hotelling's $T^2$ test. Values above the diagonal are raw p-values and those below the diagonal are corrected for multiple tests (Bonferroni's correction by multiplying p-values by the number of tests – 16). Significant p-values, indicating significant differences in the shape of wings between two sites, are shown in bold.**

| Site | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| 1 | | 0.643 | 0.632 | 0.519 | 0.384 | 0.154 | **0.004** | **0.002** |
| 2 | 17.998 | | 0.821 | 0.085 | 0.148 | 0.215 | **0.001** | **0.000** |
| 3 | 17.687 | 22.981 | | 0.354 | 0.422 | 0.236 | **0.012** | **0.001** |
| 4 | 14.542 | 2.370 | 9.901 | | 0.181 | 0.166 | **0.001** | **0.000** |
| 5 | 10.745 | 4.140 | 11.812 | 5.056 | | 0.237 | **0.012** | **0.012** |
| 6 | 4.303 | 6.013 | 6.600 | 4.651 | 6.641 | | 0.193 | **0.021** |
| 7 | 0.101 | **0.019** | 0.332 | **0.024** | 0.337 | 5.412 | | **0.047** |
| 8 | **0.044** | **0.000** | **0.020** | **0.000** | 0.330 | 0.589 | 1.303 | |

The sites were shown to vary significantly in shape using the MANOVA test in PAST (Wilk's $\lambda$ = 0.2195, $F_{196,1292}$ = 1.644, $p < 0.0001$). A comparison of the sites using Hotelling's $T^2$ test showed that specimens from site 8 (Loch of Kinnordy) were significantly different from specimens caught at all other sites (Table 9.2). After a Bonferroni correction for multiple tests, specimens from site 8 were

still significantly different from those of the four most southern sites and specimens from site 7 were significantly different from those of sites 2 and 4. This difference in shape between sites could also be seen in the canonical variates analysis plot (Figure 9.5) where sites 6, 7 and 8 became progressively more distinct from the group comprising the other five sites along the first CVA axis.

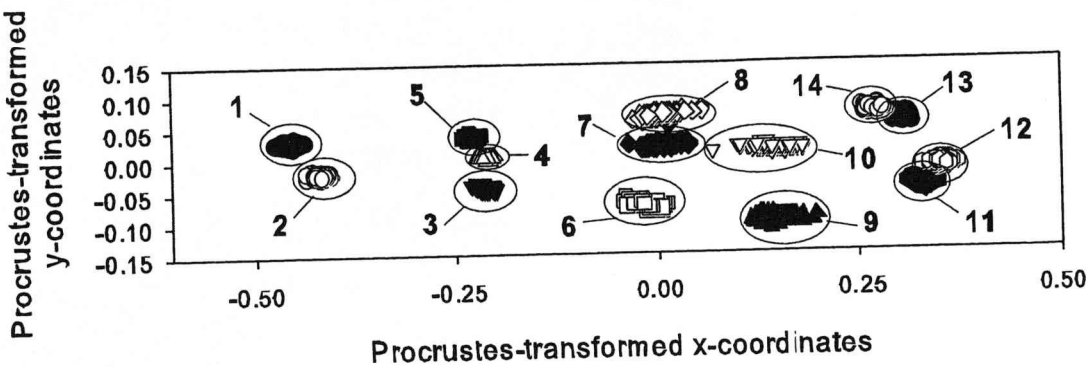


**Figure 9.3 – Variation in the locations of 14 wing landmarks in *Coenagrion puella* across eight sites after standardisation by Procrustes transformation. Numbers show clouds of points corresponding to landmarks from Figure 9.1.**

## 9.5. Discussion

Although wing venation was shown to be highly conserved between populations in the southern sites, those individuals inhabiting sites closest to the northern range margin exhibited a progressive increase in differentiation from the shape characteristic of sites closer to the core of the range. The mechanism for the variation in shape is not clear. It is likely that wing size would be closely correlated with body mass, since wing loading (the mass of an organism per unit area of wing) is an important energetic constraint.

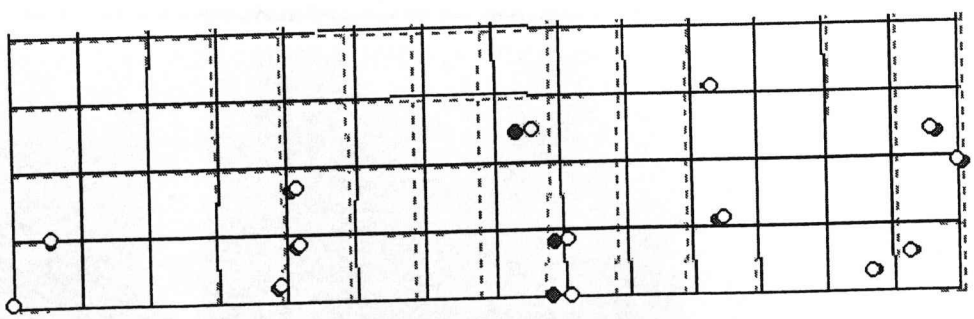

**Figure 9.4 – Superimposition of mean relative warps of *Coenagrion puella* wing shape from specimens from Kinnordy (hollow circles on solid mesh) onto those from Coronation Pit (filled circles on dotted mesh).**

An explanation could be that the wing shape exhibited by marginal populations is that which carried the initial colonisers to those sites. A founder effect can be caused by highly dispersive individuals establishing new populations with subsequent progeny inheriting those dispersal characteristics. This pattern has been demonstrated for Lepidoptera (Hill et al., 2006, Hughes et al., 2003). However, the complexity inherent within odonate flight makes it difficult to assess whether or not the change in shape confers an advantage to dispersal. In support of this hypothesis, however, *Coenagrion puella* had not been recorded at either Loch of Kinnordy or Tailend Moss prior to our visit (P. Batty pers. comm.). The short history of the species at these sites may have preserved the dispersal characteristics of the founders.

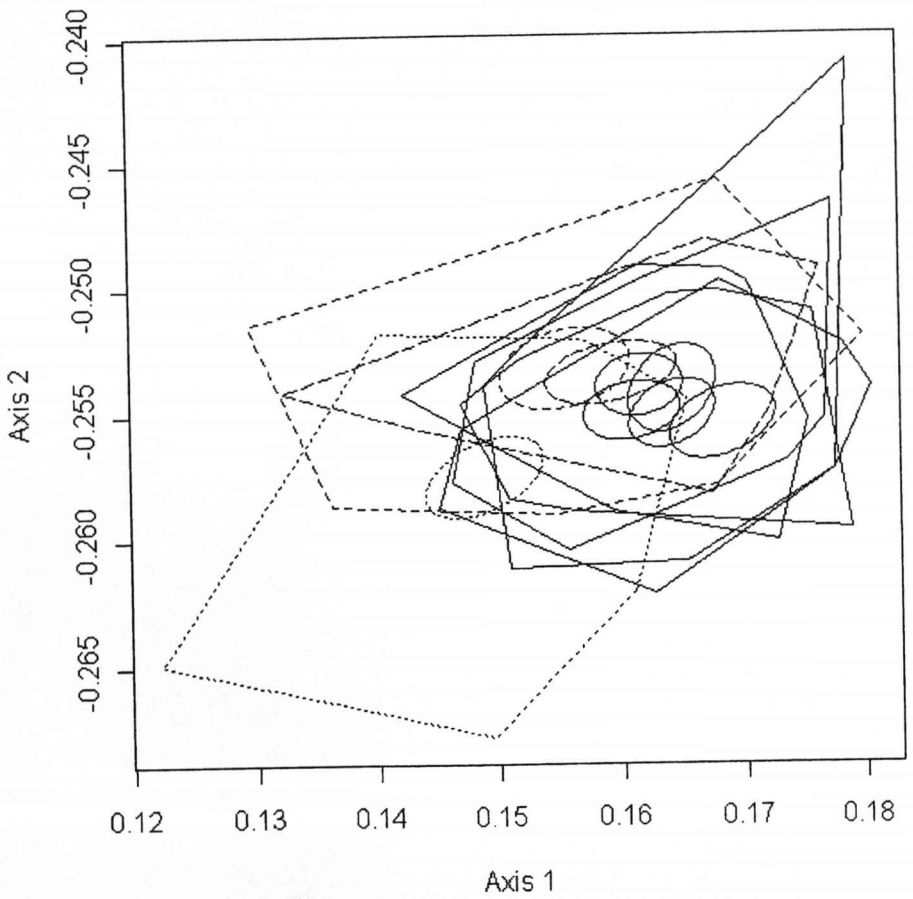


**Figure 9.5 – Ordination plot from a canonical variates analysis showing the variation in wing shape in *Coenagrion puella* at eight sites along a latitudinal transect. Polygons are convex hulls (encompassing all data points for each site) and ellipses are 95% confidence ellipses. The 5 southern sites are shown as solid lines (———), site 6 is shown as long dashes (— — —), site 7 as short dashes (--------) and site 8 as dotted lines (·····). The two axes explained 42.99% (axis 1) and 18.36% (axis 2) of the variation in the data.**

A final explanation may lie in the thermal stress under which the damselflies are developing. Environmental stressors have been linked to variation in wing shape in Lepidoptera (Hoffman et al., 2002) and fluctuating asymmetry in a wide range of species (Parsons, 1990) as well as Odonata (e.g. Chang et al., 2007). This low-temperature stress may be affecting the development of highly conserved genetic traits which may otherwise conform to the general species pattern. However, if this were the case, one would expect the variation to lack the direction that appears to be present in Figure 9.5, so the developmental instability may be directional. This second hypothesis assumes that the wing shapes exhibited by the southern populations are "ideal" and that deviations from that shape caused by thermal stress would be detrimental. Such deviations may contribute to the inability of *C. puella* to exist further north than these sites. This runs counter to the previous hypothesis, which suggested that the northern wing shape has an advantage for individuals inhabiting those sites.

Wing venation has long been used as a character to trace odonate phylogenies. This study has shown that wing shape varies between populations, even when only a relatively small proportion of vein junctions are analysed. The results of this study represent the first to demonstrate the morphometric flexibility of this trait. Care should be taken to assess intra- and inter-population variation in shape where venation is used to discriminate between closely related species.

# *Chapter 10. Determinants of odonate assemblage structure in the ponds of northwest England*

## 10.1. Abstract

An understanding of habitat requirements of individual species is essential both to quantify the number and distribution of habitat patches available to those species and to inform measures intended to conserve them. I tested four hypotheses concerning the habitat characteristics of British Odonata using an extensive survey of 488 ponds. I investigated physical, chemical and botanical factors that can influence the composition of odonate communities. I constructed multivariate models (using partial canonical correspondence analysis) to describe odonate communities in terms of (i) pond characteristics, (ii) botanical community structure, and (iii) water chemistry. A comparison of the support for the models indicated that botanical communities and pond characteristics had the greatest influence, and water chemistry had least influence. It has been proposed that plant communities provide cues that Odonata can use to assess to the nature of the pond. Multivariate models were constructed to describe the botanical community in terms of pond characteristics and water chemistry. The models did not perform sufficiently better than null models, demonstrating little support for this hypothesis. I tested putative biotic and abiotic correlates of odonate diversity. A range of factors influenced odonate species number and diversity (Shannon diversity index) when considered individually as has been done in previous analyses: water permanence, presence of amphibians, chemical oxygen demand, biochemical oxygen demand and botanical diversity. However, when this suite of factors was considered together in a single model pH and biochemical oxygen demand (BOD) were highlighted as having the greatest effect. Equivocal evidence was found for the use of odonate diversity or species number as an indicator of general species richness of a pond. While significant positive relationships existed between odonate diversity and both botanical and macroinvertebrate species richness, odonate diversity explained a low proportion of the variance in the data. I demonstrated that a range of different factors influence the structure of the odonate community but that botanical communities do not provide any indirect cues as to these factors. While Odonata should not be used in isolation as indicators of species richness, their inclusion in more complex metrics is advised due to their associations with higher diversity and high water quality. The diversity of habitats that Odonata inhabit demands the conservation of an equally diverse array of ponds to ensure the continued persistence of the full odonate fauna.

## 10.2. Introduction

The identification of associations between particular plant or animal taxa and aspects of their abiotic or biotic environment allows: (i) inferences concerning the habitat to be drawn from observations of the resident flora and fauna, and (ii) targeted conservation effort for particular species in the form of habitat amelioration. Biological indicators have been used to assess water quality (Wright et al., 2000), to infer about plant growth conditions (Ellenberg et al., 1991), and to evaluate grazing effects (Foote and Hornung, 2005). Furthermore, detailed studies of habitat requirements has led to conservation recommendations for amphibians (Baldwin et al., 2006), birds (Poulin et al., 2002), reptiles (Burke and Gibbons, 1995), insects (Carvell, 2002) and mammals (Gurnell et al., 2002).

For some species (e.g., in Lepidoptera where a particular plant species is required as a host) suitable habitat is easy to identify and can be enhanced by artificial manipulation (Gutierrez and Thomas, 2000). However, this kind of detailed knowledge is lacking concerning the habitat requirements of most species and, with a few exceptions, conservation efforts have relied on anecdotal evidence in the absence of such studies (Sutherland et al., 2004). Hence, the habitat requirements of individual species need to be updated regularly to reflect each new environment in which a species was found.

The Odonata represent a group of species that inhabit a range of types of water bodies (for a review see Corbet, 2004 pp. 9-21). Odonata feature in a number of methodologies designed to assess water quality, including in the RIVPACS scheme (Wright et al., 2000) which has been applied across Europe, in the assessment of South African biotope quality (Clark and Samways, 1996) and in the assessment of the trophic state of ponds (Menetrey et al., 2005). Odonate community richness has been shown to increase with increasing dissolved oxygen (Watson et al., 1982), with increasing pH and in the absence of fish (Bendell and McNicol, 1995), and with increasing habitat permanence (McCauley et al., 2008). British Odonate assemblages also feature in the designation of Sites of Special Scientific Interest (SSSIs) and Special Areas for Conservation (SACs) and are used by the Predictive System for Multimetrics (PSYM; Environment Agency and Ponds Conservation Trust, 2002) water quality assessment method. A detailed study of the habitat of the endangered *Coenagrion mercuriale* has also been used to test anecdotal evidence of habitat requirements and provide conservation recommendations (Rouquette and Thompson, 2005).

Habitat selection in Odonata is a hierarchical process, with selection steps occurring at the level of the landscape, the habitat, and the oviposition site (Wildermuth, 1994, Buchwald, 1994). At least the first two of these steps involves visual cues which include the presence of conspecifics (Corbet,

2004), linear polarised light reflected from water bodies (Wildermuth, 1998) and structural features, including vegetation (Wildermuth, 1992). Plant communities have been implicated either as a direct cue (a specific association with that plant) or as an indirect cue (as an indicator of particular conditions in the water body) (Buchwald, 1992). As Corbet (2004, p 13) observes: "The pervasive role played by vegetation in the dragonfly life cycle makes it likely a priori that macrophytes feature prominently among cues used for habitat selection". Some habitat associations have been documented, such as the association of *Sympetrum danae* with *Sphagnum* (Michiels and Dhondt, 1990), *Erythromma najas* with the Nymphaeaceae (Hofmann and Mason, 2005) and the identification of obligate rheophiles (e.g. *Gomphus vulgatissimus*, *Calopteryx* spp. and *Cordulegaster boltonii*). Meanwhile, other associations are cited despite the absence of explicit support in the primary literature. These include the eurytopicity of *Aeshna cyanea*, *Ischnura elegans* and *Libellula depressa* (Corbet, 1999).

Modern advances in statistical analysis have led recent studies to use ordination methods to elucidate broader patterns in odonate habitat requirements (Carchini et al., 2007, Hofmann and Mason, 2005, Schindler et al., 2003). These three studies analysed data from 21, 26 and 31 sampling sites, respectively. Carchini et al. (2007) and Hofmann and Mason (2005) analysed a combination of pond characteristics, water chemistry and macrophyte community composition whereas Schindler et al. (2003) concentrated purely on macrophytes. The above studies pointed in general terms to a few patterns, for example, the importance of eutrophication and macrophyte diversity. However, a larger number of sites would provide stronger evidence for habitat associations.

The present study establishes the habitat characteristics of British Odonata present in the northwest of England. I make use of a large number of surveyed ponds (488) with a wide range of habitat characteristics (Table 10.1). I specifically test the following hypotheses:

**Hypothesis 1**: odonate community structure is related to the nature of the habitat,
**Hypothesis 2**: botanical communities act as indirect cues as to pond characteristics / chemical variables that could be used by Odonata,
**Hypothesis 3**: pH, chemical oxygen demand (COD), biochemical oxygen demand (BOD), the presence of vertebrate predators, and water permanence affect odonate diversity, and
**Hypothesis 4**: Odonata can be used as indicators of botanical and macroinvertebrate richness.

**Table 10.1 – Variables measured as each of the three sets of variables used to describe the odonate community. Plant species were recorded according to a DAFOR scale. *=binary variable and #=categorical variable.**

| Variable set | Variables |
|---|---|
| Plant species | Algae (filamentous), Algae (planktonic), Aquatic mosses, *Chara* spp., *Nitella flexilis, Fontinalis antipyretica, Riccia fluitans, Ricciocarpus natans, Acorus calamus, Sphagnum palustre, Sphagnum recurvum, Agrostis canina, Agrostis stolonifera, Alisma plantago-aquatica, Alopecurus geniculatus, Apium inundatum, Azolla filiculoides, Callitriche brutia, Callitriche hamulata, Callitriche hermaphroditica, Callitriche obtusangla, Callitriche platycarpa, Callitriche* spp. (other), *Callitriche stagnalis, Ceratophyllum demersum, Ceratophyllum submersum, Crassula helmsii, Eleogiton fluitans, Elodea Canadensis, Elodea nuttallii, Hottonia palustris, Hydrocharis morsus-ranae, Lagarosiphon major, Lemna gibba, Lemna minor, Lemna minuta, Lemna trisulca, Myriophyllum alterniflorum, Myriophyllum aquaticum, Myriophyllum apicatum, Nuphar lutea, Nymphaea alba, Nymphaea* spp. (other), *Nymphoides peltata, Potamogeton berchtoldii, Potamogeton crispus, Potamogeton natans, Potamogeton obtusifolius, Potamogeton polygonifolius, Ranunculus aquatilis, Ranunculus hederaceus, Ranunculus omiophyllus, Ranunculus peltatus, Ranunculus trichophyllus, Sparganium* spp., *Spirodela polyrhiza, Stratiotes aloides, Zannichellia palustris* |
| Water chemistry | pH, Conductivity (µS/cm), BOD (mg/l), COD (mg/l), Ammonia (mg/l), Nitrite (mg/l), Suspended solids (mg/l), Non-volatile solids (mg/l), Alkalinity (mg/l), Chloride (mg/l), Orthophosphate (mg/l) |
| Pond characteristics | Ordinal sampling date, Latitude (°N), Longitude (°E), Altitude (m asl), Width (m), Length (m), Depth of water (m), Depth of sediment (m), % shaded by trees, % cover emergent plants, % of plants with rigid narrow leaves, % plants with flexible leaves, % true aquatic plants, % cover of all floating leaved, Banks grazed?*, Banks eroded?*, Dry up?*, Fish present?*, Fished?*, Domestic fowl present?*, Wild birds present?*, Cloudy water?*, Wetlands within 250m?*, Wetlands within 500m?*, Amphibians present?*, Drawdown (cm), Nature of pond base#, Nature of sediment# |

## 10.3. Methods

Data were collected from 488 ponds in Cheshire, UK, during annual biodiversity surveys between 1995 and 1998 (Guest and Bentley, 1995-1998) as part of the "PondLIFE Project" (Boothby, 2000). Ponds were surveyed to collect a series of datasets (Table 10.1):

(i) Botanical Survey

All submerged, floating, and emergent plants present in each pond were identified, up to the estimated maximum winter water level. Species were ranked using a DAFOR scale (Dominant, Abundant, Frequent, Occasional, Rare), with intermediate classifications (e.g. locally abundant) used where appropriate. Filamentous and planktonic algae were only recorded when a visual inspection revealed that the water was discoloured.

(ii) Macroinvertebrate Survey

Using pond nets with 1mm mesh, odonates were collected from major pond microhabitats: (i) open water, (ii) over both sediment and bare substrate, and (iii) within the leaf litter. Animals were also collected by scraping rocks and logs that were either submerged or were found within the perimeter set by the maximum winter water level. Damp poolside areas were surveyed by creating a depression and netting the resulting puddles. Sampling was continued until no further species were found (Eyre et al., 1986). Abundances were recorded using the DAFOR scale, as above.

(iii) Water Chemistry

pH, conductivity ($\mu S.cm^{-1}$), biochemical oxygen demand (BOD, $mg.l^{-1}$), chemical oxygen demand (COD, $mg.l^{-1}$), ammonia ($mg.l^{-1}$), nitrite ($mg.l^{-1}$), suspended solids ($mg.l^{-1}$), non-volatile solids ($mg.l^{-1}$), alkalinity ($mg.l^{-1}$), chloride ($mg.l^{-1}$) and orthophosphate ($mg.l^{-1}$) were measured at the National Rivers Authority Environmental Laboratory, Nottingham, UK.

(iv) Pond characteristics

Ponds were physically characterised by visual survey for most variables. Pond permanency, grazing by livestock of banks, presence of fish, and the occurrence of fishing were determined through consultation with the land owner. Altitude was determined ±5m from Ordnance Survey maps. Water depth, sediment depth, and type of sediment were determined by probing with a pond net handle. Amphibia were searched for as eggs, larvae, and adults both in the water and around the pond margins. Newt eggs were searched for in both aquatic vegetation and fallen leaves. Each pond was netted for 15 minutes or more in line with published guidelines (Hayes and Whitehurst, 2001). These data will hereafter be referred to collectively as the "pond characteristics".

### 10.3.1. Statistical Analysis

DAFOR (Dominant Abundant Frequent Occasional Rare) classifications of plants and Odonata larvae were converted to numerical values using the ordinal transform scale and then to % cover following the methods of van der Maarel (2007). In order to aid the legibility of figures, Odonata species are referred to throughout by three-letter codes, the key to which is located in the legend to Figure 10.1. Frequencies of individual species occurrence and the number of species per pond were calculated using the full dataset of 488 ponds.

**Table 10.2 – Numbers of ponds used in each of the statistical tests. Numbers in brackets are the numbers of species of plants or odonates or the number of variables measured for pond characteristics and water chemistry.**

| Hypothesis | Response | Environment | Number of ponds |
|---|---|---|---|
| 1 | Odonate community (14) | Plant community (68) | 293 |
| | Odonate community (14) | Pond characteristics (26) | 260 |
| | Odonate community (10) | Water chemistry (11) | 53 |
| 2 | Plant community (38) | Water chemistry (9) | 72 |
| | Plant community (66) | Pond characteristics (26) | 300 |

**Hypotheses 1 and 2 –** Multivariate analyses

Ponds were only included in the multivariate analyses if they contained at least one of the species from the community of interest (plants or odonates) and data for the environmental predictors. This reduced the numbers of ponds that could be analysed, which are summarised in Table 10.2 along with the number of species/variables featuring in each analysis. Water chemistry data were log-transformed where Anderson-Darling tests demonstrated a significant deviation from normality (ammonia, nitrite, suspended solids, suspended non-volatile solids, chloride and orthophosphate).

Partial constrained correspondence analysis (pCCA) models were constructed to model community composition in each of the analyses after partialling out variation due to date, latitude, longitude and altitude. Beginning with a null model, variables were added or removed until the Akaike Information Criterion (AIC) was minimised. The model terms were then tested for significance using ANOVA. In the case of the pond characteristics, two categorical variables ("nature of pond base" and "nature of sediment") were excluded as CCA cannot handle categorical variables. The explanatory power of the models was checked by calculating ΔAIC values relative to those of the null models created during model construction. As a rule of thumb when comparing the relative merits

of models, $\Delta AIC \leq 2$ shows considerable support, $4 \leq \Delta AIC \leq 7$ shows considerably less support, and $\Delta AIC \leq 10$ have essentially no support (Burnham and Anderson, 2004).

Three different datasets of environmental variables were used to describe odonate communities: pond characteristics, botanical communities and water chemistry. Further analyses were conducted to describe plant communities in terms of water chemistry and pond characteristics (see Table 10.2 for a schematic of the analyses). All statistical analyses were carried out using the "vegan" package (Oskanen et al., 2007) in R (R Development Core Team, 2006). A comparison was made between the water chemistry data and mean pond Ellenberg values for "reaction" (equivalent to pH), nitrogen and salinity using values adjusted for use with British plants (Hill et al., 1999b) in 66 ponds with the appropriate data.

Chi-squared tests were used to reveal associations between odonates and plant species. In particular, I tested for associations demonstrated in previous studies between *Sphagnum* and *Sympetrum danae* and between the Nymphaeaceae and *Erythromma najas*.

**Hypotheses 3 and 4** – Correlates of odonate diversity

The factors that had been proposed as having an effect on odonate communities were investigated: presence of fish (n=260), presence of amphibians (n=260), water permanence (n=260), pH (n=69), BOD (biochemical oxygen demand, n=53), COD (chemical oxygen demand, n=53), plant diversity (n=293) and plant species number (n=293). Odonate species number and diversity (Shannon diversity index) were analysed against each of these variables using the Mann-Whitney U-test for the first three binary variables and Spearman's rank correlation for the four continuous variables. An extended dataset of 123 ponds was used to assess the difference in pH between ponds containing and not containing fish using a Mann-Whitney U-test. An ANCOVA was used to test for the significance of all binary and continuous variables in a single model using ponds for which all data were available (n=50). Macroinvertebrate diversity and species number were also regressed against odonate diversity and species richness using Spearman's rank correlation (n=279).

**Table 10.3 – Factors selected to describe odonate communities by stepwise AIC model creation. Significant terms are highlighted in bold. See Table 10.4 for a key to abbreviations. Only terms where p<0.1 are shown for the botanical analysis – other terms selected for the model with p>0.1 are H_pa, N_pe, F_an, R_ni, S_pe, A_st, R_fl, C_sp, A_gl, S_rei, M_al, A_ge, Alg_f, C_ha, C_de, S_po.**

| Plant community | | | Pond characteristics | | | Water chemistry | | |
|---|---|---|---|---|---|---|---|---|
| Factor | F | P | Factor | F | P | Factor | F | P |
| **P_po** | **6.886** | **0.004** | **%EP** | **0.3403** | **<0.001** | **COD** | **1.2060** | **0.019** |
| **A_fi** | **6.422** | **0.006** | **Wid** | **0.3319** | **0.003** | pH | 0.6578 | 0.087 |
| **A_pl** | **5.563** | **<0.001** | **WBirds** | **0.2472** | **<0.001** | Alk | 0.4821 | 0.251 |
| **S_re** | **4.253** | **0.022** | **WP** | **0.2458** | **0.004** | Cl | 0.3652 | 0.419 |
| **Z_pa** | **3.764** | **0.039** | **WDep** | **0.1774** | **0.004** | | | |
| **N_lu** | **3.629** | **0.014** | %.Shade | 0.1192 | 0.093 | | | |
| **A_in** | **3.183** | **0.036** | Fish | 0.1183 | 0.076 | | | |
| **R_he** | **2.909** | **0.038** | %FLP | 0.1082 | 0.135 | | | |
| **E_ca** | **2.393** | **0.046** | %Float | 0.1308 | 0.058 | | | |
| Alg_p | 2.501 | 0.067 | Amph | 0.1050 | 0.160 | | | |
| C_pl | 2.172 | 0.081 | | | | | | |
| S_ci | 2.096 | 0.086 | | | | | | |
| **Null AIC** | 1516 (edf=76) | | **Null AIC** | 1473 (edf=5) | | **Null AIC** | 269.8 (edf=19) | |
| **Final AIC** | 1475 (edf=104) | | **Final AIC** | 1457 (edf=15) | | **Final AIC** | 263.9 (edf=23) | |
| **ΔAIC** | 41 | | **ΔAIC** | 16 | | **ΔAIC** | 5.9 | |

## 10.4. Results

The percentage of ponds in which odonates were present varied between species from 0.4% in *Brachytron pratense* to 42.0% in *Coenagrion puella* (Figure 10.1A). Two ponds contained nine odonate species, although the majority (53.3%) contained no or one species (Figure 10.1B).

**Hypothesis 1 –** Determinants of odonate community structure

Models describing odonate communities contained 10 pond characteristics, 13 plant species, and 4 water chemistry variables (Table 10.3 and Figure 10.2). ΔAIC values for the final models (relative to the null models) showed that the botanical and pond characteristics models have substantially more support than their null models (ΔAIC = -41 and ΔAIC = -16, respectively), whereas the water chemistry model had slightly less support (ΔAIC = -5.9).

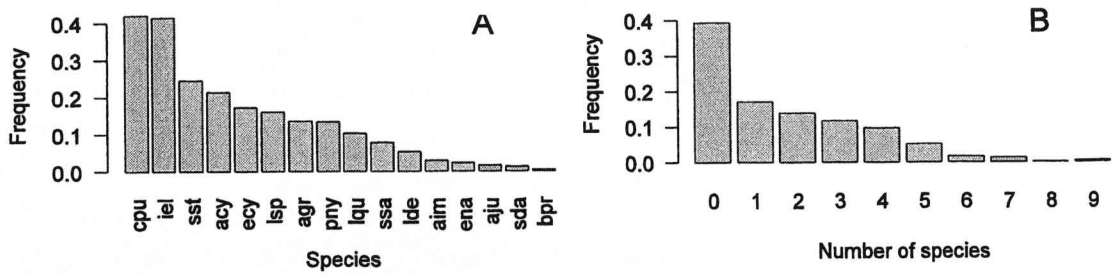


**Figure 10.1 – (A) The proportion of ponds (total=488) in which each of the 16 recorded Odonata occurred and (B) the proportion of ponds containing different numbers of odonate species. Species codes are as follows: cpu=*Coenagrion puella*, iel=*Ischnura elegans*, acy=*Aeshna cyanea*, sst=*Sympetrum striolatum*, pny=*Pyrrhosoma nymphula*, ecy=*Enallagma cyathigerum*, agr=*Aeshna grandis*, lsp=*Lestes sponsa*, lqu=*Libellula quadrimaculata*, ssa=*Sympetrum sanguineum*, ena=*Erythromma najas*, lde=*Libellula depressa*, aju=*Aeshna juncea*, sda=*Sympetrum danae*, aim=*Anax imperator*, bpr=*Brachytron pratense*.**

Chi-squared analysis demonstrated significant associations between *Sphagnum recurvum* and both *Sympetrum danae* ($\chi^2$=151, p<0.001) and *Aeshna juncea* ($\chi^2$=29.5, p<0.001). *Pyrrhosoma nymphula* was significantly associated with *Potamogeton polygonifolius* (Potamogetonaceae) ($\chi^2$=8.52, p=0.004). *Erythromma najas* did not show a significant relationship with *Nuphar lutea* ($\chi^2$=0.124, p>0.05) or the pooled Nymphaeaceae (*N. lutea*, *Nymphoides peltata* (Nymphaeaceae) and unidentified *Nymphaea* species; $\chi^2$=0.085, p>0.05). However, Figure 10.2A shows that *E. najas* is in the same quadrant of the plot as *N. lutea*.

**Hypothesis 2 –** Indirect cues to pond characteristics and water chemistry

The models that were selected to describe the plant communities in terms of water chemistry and pond characteristics contained one and five variables, respectively (Table 10.5). ΔAIC values for the two models were 1 and 3, suggesting that neither model had significant explanatory power. Mean pond Ellenberg values showed almost no significant relationships with their water chemistry equivalents (pH vs. Ellenberg reaction: r=-0.162, p=0.195; nitrite vs. Ellenberg nitrogen: r=-0.101, p=0.420; chloride vs. Ellenberg salt: r=0.115, p=0.359; conductivity vs. Ellenberg salt: r=0.249, p=0.044). The final correlation between conductivity and Ellenberg salt is non-significant after Bonferroni correction for multiple tests.

**Table 10.4 – Abbreviations used in ordination plots and models.**

| Dataset | Abbreviation | Species/factor |
|---|---|---|
| Plants | A_fi | Azolla filiculoides |
| | A_ge | Alopecurus geniculatus |
| | A_gl | Alnus glutinosa |
| | A_in | Apium inundatum |
| | A_pl | Alisma plantago-aquatica |
| | A_st | Agrostis stolonifera |
| | Alg_f | Algae - filamentous |
| | Alg_p | Algae - planktonic |
| | C_de | Ceratophyllum demersum |
| | C_ha | Callitriche hamulata |
| | C_pl | Callitriche platycarpa |
| | C_sp | Callitriche sp. |
| | E_ca | Elodea canadensis |
| | F_an | Fontinalis antipyretica |
| | H_pa | Hottonia palustris |
| | M_al | Myriophyllum alterniflorum |
| | N_lu | Nuphar lutea |
| | N_pe | Nymphoides peltata |
| | P_po | Potamogeton polygonifolius |
| | R_fl | Riccia fluitans |
| | R_he | Ranunculus hederaceus |
| | R_ni | Ribes nigrum |
| | S_ci | Salix cinerea |
| | S_pe | Salix pentandra |
| | S_po | Spirodela polyrhiza |
| | S_re | Sphagnum recurvum |
| | S_rei | Salix x reichardtii |
| | Z_pa | Zannichellia palustris |
| Pond characteristics | %EP | % cover of emergent plants |
| | Wid | Width of pond |
| | WBirds | Presence of wild birds |
| | WP | Water permanence |
| | WDep | Water depth |
| | %.Shade | % shade over pond |
| | Fish | Presence of fish |
| | %FLP | % cover of plants with flexible leaves |
| | %Float | % cover of all floating leaved plants |
| | %TAP | % cover of total aquatic plants |
| | Drawdown | Total variation in water level |
| | W500m | Presence of other water bodies within 500m |
| | Amph | Presence of amphibians |
| Water chemistry | COD | Chemical oxygen demand |
| | pH | pH |
| | Alk | Alkalinity |
| | Cl | Chloride concentration |

**Hypotheses 3 and 4 –** Correlates of odonate diversity

The presence of fish did not affect either odonate diversity (U=8749, p=0.603) or odonate species number (U=8860, p=0.475). Ponds containing amphibians had a significantly higher diversity (U=7331, p=0.013) and species number (U=7269, p=0.017) of odonates. Ponds with a history of drying up contained a significantly lower diversity of odonates (U=2572.5, p=0.006) and a significantly lower number of species (U=2512, p=0.003). pH was significantly higher in ponds that contained fish than in those that did not (U=2451.5, p<0.001).

Plant diversity was significantly correlated with odonate diversity (ρ=0.411, p<0.001). A similar relationship was found between macroinvertebrate diversity and odonate diversity (ρ=0.411, p<0.001). COD and BOD were significantly and negatively correlated with odonate diversity (COD: ρ=-0.393, p=0.004; BOD: ρ=-0.410, p=0.002). However, $R^2$ values derived from linear regressions of the ranks in these correlations ranged from 0.14 to 0.17, suggesting extremely low explanatory power of those relationships. pH was not significantly related to odonate diversity (ρ=-0.133, p=0.277).

When all seven variables were entered into a single model, pH and BOD consistently showed the strongest relationship with both odonate species number and odonate diversity (Table 10.6) with greater diversity and species numbers at higher pH and lower BOD. Plant diversity also showed a positive but non-significant trend with both response variables.

## 10.5. Discussion

### 10.5.1. Characterising habitat preferences

This study has illustrated the need to classify habitat in terms of the specific needs of individual species. The pond landscape of the northwest of England, although extremely well-connected at a coarse scale of classification, represents a network of extremely diverse habitats of which varying proportions are suitable for different species.

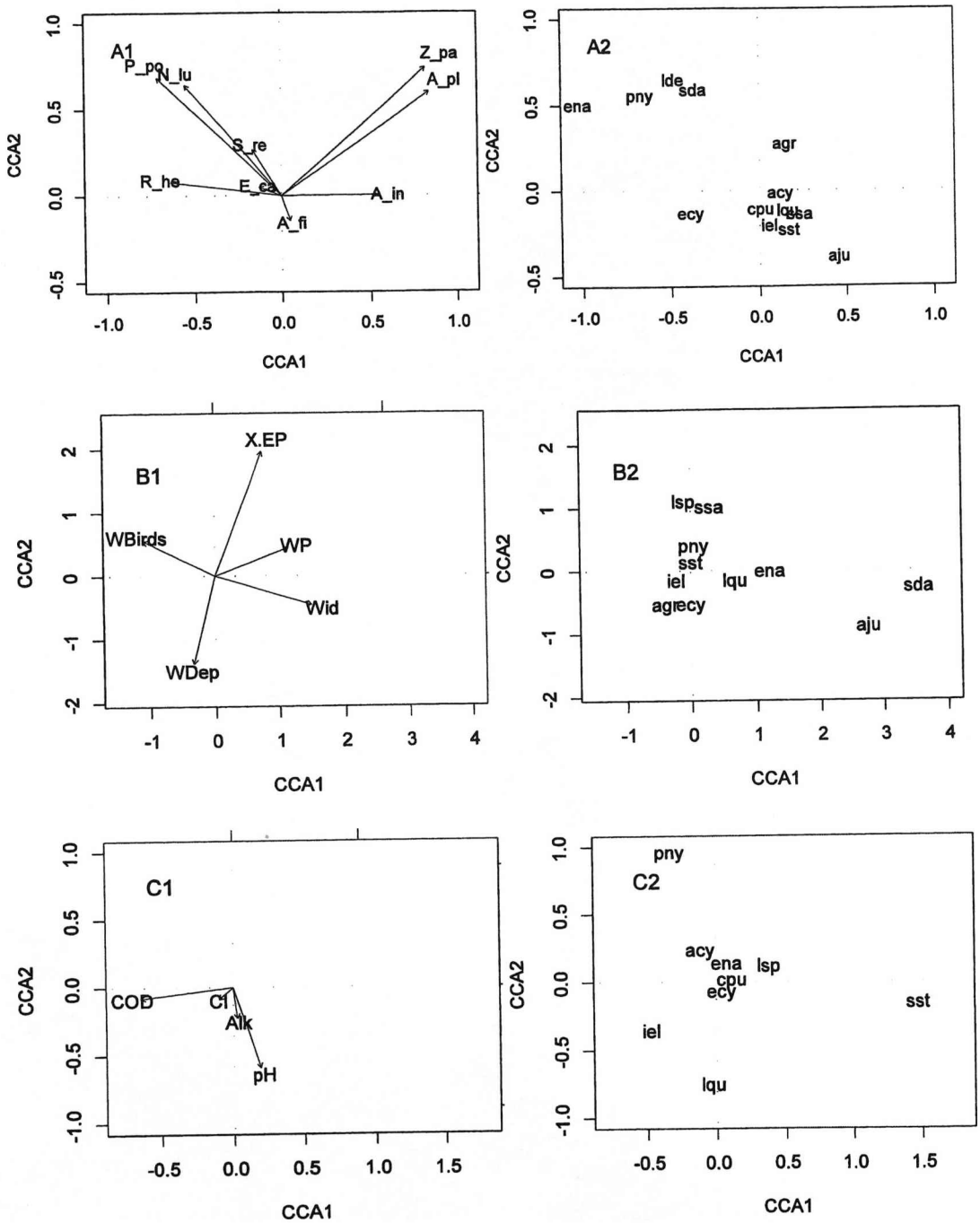


**Figure 10.2 – The results of partial constrained correspondence analyses (pCCAs) for (A) plant communities, (B) pond characteristics and (C) water chemistry explaining odonate communities, each controlling for location of pond and date of sample. To enhance clarity only significant factors are shown and some species/factors are omitted: acy (-0.13,0.08), cpu (-0.12,-0.10) and lde (-0.10,-0.53) are omitted from B2 and ssa (0.18, -0.06) is omitted from C2. See Table 10.4 for a key to the abbreviations used for environmental variables and the legend to Figure 10.1 for abbreviations of Odonata.**

**Table 10.5 – Factors selected to describe botanical communities by stepwise AIC model creation. Significant terms are highlighted in bold. See Table 10.4 for a key to abbreviations.**

| Pond characteristics | | | Water chemistry | | |
|---|---|---|---|---|---|
| Factor | F | P | Factor | F | P |
| **%EP** | **0.6788** | **<0.001** | **pH** | **1.5194** | **<0.001** |
| **%TAP** | **0.5823** | **<0.001** | | | |
| **%Float** | **0.4976** | **0.001** | | | |
| **Drawdown** | **0.6015** | **0.018** | | | |
| W500m | 0.5699 | 0.057 | | | |
| **Null AIC** | 2357 (edf=5) | | **Null AIC** | 549.7 (edf=5) | |
| **Final AIC** | 2354 (edf=6) | | **Final AIC** | 548.7 (edf=10) | |
| **ΔAIC** | 3 | | **ΔAIC** | 1 | |

This variation in the requirements of particular species within what is ostensibly a uniform environment highlights the importance of understanding species-specific habitat characteristics. Not only will such knowledge aid in active conservation measures and habitat amelioration, but it will also inform predictions of each species' ability to respond spatially to changes in climate. The impact of changes in freshwater distributions has received attention in the past (Dawson et al., 2003) and, while the loss of biodiversity resulting from the loss of particular ponds may be substantial, this study suggests that the risks to odonate persistence might be relatively small for some common species.

**Table 10.6 – Results of ANCOVAs investigating impacts of chemical and biological factors on the diversity and number of species of Odonata present in 50 Cheshire ponds ($R^2$= 27.4% for diversity, $R^2$=24.7% for species number).**

| | Odonate diversity | | Odonate species number | |
|---|---|---|---|---|
| Variable | *F* | *p* | *F* | *p* |
| pH | **4.50** | **0.040** | **5.08** | **0.030** |
| Log (BOD) | **6.01** | **0.019** | 3.95 | 0.053 |
| Log (COD) | 0.81 | 0.373 | 0.38 | 0.541 |
| Plant species number | 1.35 | 0.251 | 1.07 | 0.307 |
| Plant diversity | 3.21 | 0.080 | 3.23 | 0.080 |
| Water permanence | 1.39 | 0.245 | 0.44 | 0.510 |
| Fish presence | 0.79 | 0.380 | 0.20 | 0.656 |
| Amphibian presence | 2.46 | 0.124 | 1.61 | 0.211 |

### 10.5.2. Hypothesis 1 – Determinants of Odonata communities

#### *10.5.2.1. Botanical model*

The grouping of *Pyrrhosoma nymphula* and *Sympetrum danae* around *Potamogeton polygonifolius* and *Sphagnum recurvum* (Bryophyta: Sphagnaceae) holds with their tendency to inhabit bogs in northern England and Scotland. It is not surprising that $\chi^2$ analysis confirmed the associations of *Sympetrum danae* and *A. juncea* with *Sphagnum recurvum* given that *Sphagnum recurvum* was only present in three ponds, all of which contained *Sympetrum danae* and two of which contained *A. juncea*. *Sphagnum palustre* (Bryophyta: Sphagnaceae) was found in only one pond, in which *S. recurvum* was also present. *P. nymphula* is known to oviposit in *P. polygonifolius* (CH, *pers. obs.*). Bog specialists such as *A. juncea* and *Sympetrum danae* have been highlighted as a conservation concern in Finnish ponds due to a high rate of population extinction (Korkeamaki and Suhonen, 2002).

*Libellula depressa* had recently colonised the area at the time of the survey and so may have been limited to warmer bogs rather than other types of water bodies at its northern range margin, although there were no significant associations with either *P. polygonifolius* or *S. recurvum*. *Erythromma najas* has previously been associated with *Nuphar lutea* in an English lowland river catchment (Hofmann and Mason, 2005). Although *N. lutea* is known to be an oviposition substrate for *E. najas* there was no significant relationship in this study.

The strength of support for the botanical model compared to that of the pond characteristics and chemistry models suggests that previously observed correlations between macrophyte species number and odonate diversity might not be a simple matter of architectural complexity. Instead, the association of odonate species with particular plant species could result in the same pattern if an increase in the number of plants that are favoured by Odonata increases with increasing plant species richness. However, note that six species are clustered around the origin of the biplot in **Figure 10.2**A2, suggesting that they are eurytopic with respect to macrophytes.

#### *10.5.2.2. Pond characteristics model*

The lower left quadrant of Figure 10.2B seems to relate to deeper ponds with less emergent vegetation. *Aeshna grandis* is the only species unequivocally located in this quadrant and is known to inhabit larger lowland lakes and fens. Also in the lower half of the plot is *Enallagma cyathigerum*, which has previously been associated with deeper water (Carchini et al., 2005). In contrast, the upper right quadrant relates to shallow, temporary ponds with a high cover of emergent vegetation.

*Sympetrum sanguineum*, a species known to inhabit temporary ponds (Carchini et al., 2007) as well as shallow, well-vegetated lakes and turloughs, is the only unequivocal species. This is located close to *Lestes sponsa*, which also possesses adaptations to temporary waters. A relatively weak effect of environmental variables was also reported in Carchini et al. (2005).

#### *10.5.2.3. Chemical model*

While the water chemistry model lacked explanatory power, the horizontal axis of Figure 10.2C, being characterised mainly by a gradient in chemical oxygen demand (COD), appears to accurately place *Ischnura elegans* and *Sympetrum striolatum* at opposite ends of the eutrophication scale. *I. elegans* is known to be remarkably tolerant to organic pollution (Dumont and Dumont, 1969) while *S. striolatum* actively avoids eutrophic water bodies. The eurytopicity of *I. elegans* was also noted in Austrian ponds (Schindler et al., 2003).

### 10.5.3. Hypothesis 2 – Indirect cues of pond characteristics and chemistry

There was little evidence that botanical cues could be used as indirect indicators of either pond characteristics or chemical conditions within water bodies. Indeed, water chemistry variables predicted from plant communities using modified Ellenberg indicators appear to exhibit no relationship with the actual water chemistry measurements taken from the ponds. This runs contrary to previous suggestions (Wildermuth, 1994, Buchwald, 1992). Plants vary in their habitat requirements in different parts of their range, making regionally adjusted values for Ellenberg's indicators necessary (Hill et al., 1999b). Whether the variation in odonate habitat requirements is a manifestation of a similar regional adjustment in the preferences of odonates is unclear, but this phenomenon has been suggested in the past (Buchwald, 1989).

### 10.5.4. Hypothesis 3 – Correlates of Odonata diversity

#### *10.5.4.1. pH*

pH has been implicated in determining odonate species diversity in previous studies (Hinden et al., 2005, Bendell and McNicol, 1995), a result supported by this study. The effect of pH on odonates has been hypothesised to act indirectly via the exclusion of fish since some species of odonates are tolerant of low pH (Hudson and Berrill, 1986) but fish diversity declines with decreasing pH (Tremblay and Richard, 1993). This study found that pH is significantly lower in ponds without fish, supporting this reasoning. However, there was no effect of fish presence on the diversity of odonates.

Further evidence for a role for pH in structuring odonate communities comes in its selection in both the water chemistry pCCA model and the model describing plant communities in terms of water chemistry (although the explanatory power of this model did not difference substantially from the null model suggesting that plants are not indirect cues to water chemistry). pH has not been associated with odonate communities in previous analyses (Hofmann and Mason, 2005, Carchini et al., 2007, Carchini et al., 2005, Schindler et al., 2003).

#### *10.5.4.2. Water permanence*

Some species of Odonata possess traits which promote persistence in temporary water bodies including increased growth rates and drought-tolerant eggs in *Lestes* spp. (De Block et al., 2008a). However, only one of the species considered in this study (*Lestes sponsa*) possessed such traits. The greater odonate diversity in permanent ponds relative to temporary ponds is not surprising, given that at least seven out of the 14 species included are semivoltine (estimated using the appendix in Corbet et al., 2006) and therefore require an extended hydroperiod to reach emergence, and that permanent water bodies tend to be larger and therefore contain a greater diversity of microhabitats. Aside from macrophyte diversity, water permanence is the most consistent variable affecting odonate diversity (Carchini et al., 2007, Schindler et al., 2003, Clark and Samways, 1996).

#### *10.5.4.3. Amphibian presence*

A greater diversity of odonates in ponds containing amphibians suggests that the two taxa have similar preference for habitat. This suggests co-variation in the response to environmental variables, which has been suggested previously (Carchini et al., 2005).

#### *10.5.4.4. Trophic state*

A range of different measures of water quality have been found to correlate with odonate richness, including ammonia concentration (Carchini et al., 2005), nitrogen concentration (Carchini et al., 2007) and biochemical oxygen demand (Hofmann and Mason, 2005). BOD was shown to be significantly and negatively related to odonate diversity in this study. A similar relationship was present with odonate species number but this was not significant.

### 10.5.5. Hypothesis 4 – Odonata as indicators of botanical or invertebrate richness

Almost all previous studies investigating odonate richness or diversity have found a significant correlation with botanical diversity (Schindler et al., 2003, Carchini et al., 2007, Carchini et al., 2005, Scher and Thiery, 2005, Hofmann and Mason, 2005, Clark and Samways, 1996). However, I find a very weak relationship between the two variables. This is further evidence for a combined effect of

both structural complexity and particular botanical associations in determining odonate communities.

### 10.5.6. Conservation concerns

In the time that has elapsed since the collection of the data, Odonata have been shifting their ranges poleward (Hickling et al., 2006). This expansion has almost certainly altered the distribution of this taxon throughout the region, rendering conservation advice based on this data out-of-date. However, an important point to note is that species may appear relatively rare in a region at the edge of the range purely as a result of the highly fragmented nature of marginal habitat. The fragmentation of habitat at range margins has been both predicted from models (Travis and Dytham, 2004, Thomas et al., 1999) and observed in natural systems (Roy and Thomas, 2003). A variation in what constitutes viable habitat between core and marginal sites may explain regional variation in odonate habitat requirements (Buchwald, 1989).

### 10.5.7. Recommendations for future work

The description of odonate habitat is a complex task made more difficult by the lack of standardised sampling methods, the spatial disparity of sampled sites and the apparent idiosyncrasies in the relationships between Odonata and habitat variables (Carchini et al., 2005). This problem is compounded by the questionable use of adults in such surveys (Scher and Thiery, 2005, Hofmann and Mason, 2005). The presence of an adult and even the exhibition of reproductive behaviour are not guarantees that the water body represents a viable habitat. Larvae and exuviae are the only reliable indicators of reproduction and exuviae are the only reliable indicator of an entire life cycle being possible within a given habitat. To remedy some of these problems, I recommend the adoption of standard pond survey techniques, as laid out in the UK National Pond Survey methods (Pond Action, 1998), or river survey techniques as used in RIVPACS (Wright et al., 2000).

## 10.6. Conclusions

Of the theories posited to explain community structure in Odonata, botanical associations appear to exert the strongest influence, followed by pond characteristics and finally a weak effect of water chemistry. Contrary to previous suggestions, there was no evidence of botanical assemblages acting as indirect cues to either water chemistry or pond characteristics. Odonate diversity was most strongly influenced by pH and biochemical oxygen demand. There was a significant though very weak relationship between macrophyte, macroinvertebrate and odonate diversity suggesting that the Odonata are not suitable for use in isolation as indicators of general species richness. Conservation concerns only arise over the fate of a few more specialised species, although I would

warn against extensive habitat alteration until Cheshire forms a more central part of the rarer species' ranges. Further study is required on the biotic interactions within pond communities if we are to determine their structure and the potential use of their constituent taxa as indicators of ecological or environmental variables.

# *Chapter 11. Environmental change and higher trophic levels in aquatic ecosystems of northwest England*

## 11.1. Abstract

Fish traditionally occupy the niche of top predator in permanent aquatic ecosystems. As the environment warms and patterns of precipitation change, a transition will occur from permanent to non-permanent water bodies and, under such circumstances, species that are less susceptible to hydroperiodic fluctuations will increase in prominence. In this study I use extensive datasets to predict changes in the higher trophic levels in British aquatic ecosystems under environmental warming. Extensive pond macroinvertebrate surveys were carried out at 449 ponds in Cheshire, UK. Macroinvertebrate species richness was not affected by pond area but was 54% higher in permanent ponds (mean = 30.4 ±0.70 (SE) species) compared to non-permanent ponds (mean = 19.8 ±0.92 species). Among the 375 species that were recorded were representatives of fish, amphibians, Anisoptera (Odonata), Zygoptera (Odonata), Hirudinea (Annelida), Notonectidae (Hemiptera), Tricladida (Platyhelminthes), Corixidae (Hemiptera) and Dystiscidae (Coleoptera), all of which taxa contain predatory species. Sensitivity to hydroperiodic fluctuations was investigated by testing each taxon for a significant association with permanent (343 ponds) or non-permanent (106 ponds) water bodies. Fish were found to be most affected, inhabiting 45% of permanent ponds and only 9% of non-permanent ponds. Amphibians (64% permanent vs 58% non-permanent) and Dysticidae (96% permanent vs 92% non-permanent) were the only taxa that were not significantly affected. Using MANOVA, macroinvertebrate communities were shown to be similar between permanent and non-permanent water bodies but to vary with the presence or absence of fish. Estimates were made of maximum body sizes for macroinvertebrates found in the surveys. Data from the literature were used to estimate the size range of prey that each predatory group was capable of handling. Fish and Dytiscidae were capable of handling 100% and 97.2%, respectively, of potential macroinvertebrate prey. Again using data from the literature, diet composition was estimated for each of the nine groups of predators. MANOVA showed that there was a significant difference between the diet compositions of the nine predatory groups. A comparison of diet compositions using plots of a principal components analysis suggested that there were strong similarities between (i) Hirudinea and Tricladida, (ii) Anisoptera and Zygoptera, and (iii) Dytiscidae and fish in terms of the taxonomic composition of the diet. This study provides multiple strands of ecological evidence for the prediction of a transition from ecosystems dominated by vertebrate predators to those in which approximately the same trophic niches are occupied by invertebrates, particularly widespread Dytiscidae.

## 11.2. Introduction

Much of the focus of research into the biological impacts of climate change has centred on the role that increasing environmental temperature plays in influencing biological processes (Parmesan, 2006). However, concomitant changes in a range of other climate variables will also result in substantial impacts on the global biota. Both aquatic and terrestrial habitats will experience variation in patterns of precipitation, which in mid-latitudes will manifest as a decline in annual precipitation (IPCC, 2007).

Previous fluctuations in climate have produced spatially correlated patterns in lake water levels at a regional scale (Harrison, 1989). Future changes in water availability have been predicted to result in seasonal stresses in some areas of the UK (Dawson et al., 2003). Such fluctuations will have considerable consequences for the aquatic ecosystems existing therein. However, small water bodies such as ponds may experience not only a change in water level but also a change in hydroperiod, the timing and duration of the presence of water in the water body. Temporary and permanent aquatic communities have been shown to vary widely, with the former containing organisms that have adaptations to allow persistence in discontinuous hydroperiods (Collinson et al., 1995, Wellborn et al., 1996). Such adaptations include physiological tolerance, life history modification and migration (Williams, 1997).

The pressure of a decrease in precipitation combined with increased evaporation resulting from increases in environmental temperature is certain to result in a decline in the proportion of permanent ponds. However, the extent of the transition can take one of three forms: (i) "episodic" drying where hydroperiod varies unpredictably, (ii) "intermittent" drying where hydroperiod varies predictably, or (iii) complete drying leading to succession to terrestrial habitat. A gradual decline in hydroperiod (or increase in drying probability) will mean that most transitional ponds pass through the episodic phase where occasional drying events lead to an unpredictable hydroperiod.

In river systems, a climate-induced decline in flow has been predicted to result in an increase in the rate of fish extinctions (Xenopoulos and Lodge, 2006, Xenopoulos et al., 2005). The decline in flow can be assumed – for qualitative purposes – to be analogous to the decline in pond permanence. This decline in fish diversity resulting from drying has been shown in lentic systems to enhance macroinvertebrate communities (Dorn, 2008).

Even without changes in water permanence, aquatic communities are likely to change. Increases in water temperature in line with those predicted by climate models (3°C above ambient) were shown not to affect macroinvertebrate communities in experimental mesocosms (Feuchtmayr et al., 2007). The same study showed that a common UK fish species (*Gasterosteus aculeatus* (Actinopterygii)) significantly reduced the abundance of most macroinvertebrate taxa. Increased temperature and nutrient addition had a negative effect on fish biomass individually and a combination of those treatments resulted in fish extinction (Moran et al., in press). *G. aculeatus* is tolerant to high temperatures compared to other British fish (Froese and Pauly, 2008). The increase in nutrients actually resulted in increases in abundances of four groups of macroinvertebrates.

Thus a situation may arise in which fish, the group which contributes most to the determination and maintenance of community structure in freshwaters (Bendell and McNicol, 1995), are threatened by a range of pressures. The rate of colonisation of lentic water bodies by fish is relatively low apart from in unmodified floodplains (Corti et al., 1997). This is further impeded by the presence of geographical barriers such as the English Channel which prevents patterns of colonisation observed elsewhere (Daufresne and Boët, 2007). These pressures may have negligible impacts on the invertebrate communities of those same freshwaters as described above. Predators are known to give stability to the ecosystems that they inhabit in the face of climate change (Wilmers and Getz, 2005, Sala, 2006) and so the question needs to be addressed as to which taxa will fill the highest trophic niche.

Here I briefly address the relative susceptibility of aquatic predators (fish, amphibians and invertebrates) to water permanence using extensive field surveys and the similarity in their diet in terms of both the range of prey sizes that they can handle and taxonomic composition using laboratory studies. In ponds of northwest England, Dytiscidae (Coleoptera) are shown to be both widespread and largely unaffected by water permanence. Aquatic macroinvertebrate predators in general are less affected by water permanence than fish, although (apart from the Dytiscidae) they may lack the prey size range to fill the top predator niche. It is concluded that predatory diving beetles represent a taxon which is equivalent to fish in terms of prey size distribution and taxonomic preferences while being considerably more resistant to the effects of climate change. This family may, therefore, represent a group that dominates in ecologically transitional aquatic ecosystems.

## 11.3. Methods

### 11.3.1. Sensitivity to water permanence

488 ponds were surveyed between 1995 and 1998 in Cheshire, UK, as part of the PondLIFE project (Guest and Bentley, 1995-1998). The presence and absence of macroinvertebrate species was recorded using standardised sampling methods. Pond nets with 1mm mesh were used to collect macroinvertebrates in the following microhabitats: (i) open water, (ii) over both sediment and bare substrate, and (iii) within the leaf litter. In addition, animals were collected through the scraping of rocks and logs that were either submerged or were found within the perimeter set by the maximum winter water level. Damp poolside areas were surveyed by creating a depression and netting the resulting puddles. The rationale behind the sampling was to continue surveying until no further species were found (Eyre et al., 1986).

Ponds were classified as (i) permanent, (ii) known to dry out or (iii) annually drying out. Due to uncertainties over the extent of drying, categories (ii) and (iii) were pooled as "non-permanent" ponds and 39 ponds were excluded. The presence and absence of nine groups of aquatic predators (fish, amphibians, Anisoptera (Odonata), Zygoptera (Odonata), Dytiscidae (Coleoptera), Corixidae (Hemiptera), Notonectidae (Hemiptera), Hirudinea (Annelida) and Tricladida (Platyhelminthes)) were analysed in relation to the two categories of water permanence using $\chi^2$.

### 11.3.2. Predators, permanence and aquatic macroinvertebrates

Macroinvertebrate communities were surveyed and animals identified to species in 488 ponds in northwest England between 1995 and 1998 (Guest and Bentley, 1995-1998). 436 ponds could be classified with confidence as (i) either permanent water or with a history of drying up and (ii) fishless or containing fish. The presence of macroinvertebrates was recorded using a semi-quantitative dominant-abundant-frequent-occasional-rare (DAFOR) scale and then converted to numerical values using the ordinal transform scale followed by a conversion to % cover following the methods of van der Maarel (2007). Mean abundance values were found for each family of macroinvertebrates to reduce the number of dependent variables. A canonical correspondence analysis (CCA) model of macroinvertebrate communities was built with water permanence (permanent/non-permanent) and fish presence/absence as factors and this model was tested for significance using a permutation test for analysis of variance (ANOVA) with 10,000 permutations. Posthoc comparisons of treatment combinations were carried out using multivariate analysis of variance (MANOVA). Non-metric multidimensional scaling (NMDS) was performed using the metaMDS command in the "vegan"

package (Oskanen et al., 2007) in R (R Development Core Team, 2006) to graphically present the community data.

An effect of fish presence on macroinvertebrate species richness was tested for using a general linear model (GLM) with fish presence and hydroperiod (permanent vs. non-permanent) as factors in the model. Pair-wise comparisons between the four treatments were assessed using Tukey posthoc tests. ANCOVA was used to investigate species-area effects with area of the pond as a covariate and water permanence as a factor.

### 11.3.3. Size distribution of pond communities

The diet breadth of the chosen predatory taxa was compared to the actual size distribution of potential prey items in the environment. 370 macroinvertebrate species were recorded in the PondLIFE surveys mentioned above. These belonged to 78 families within 13 orders. Detailed morphometric data do not exist for the majority of species and so a literature search was conducted for maximum body size of each family.

### 11.3.4. Diet breadth

To compare the range of prey sizes that were taken by the groups of aquatic predators, the supplementary material to Brose et al.'s (2006) study of consumer and resource body size (available at http://www.esapubs.org/archive/ecol/E086/135) was analysed. Records for freshwater ecosystems were extracted for those groups of predators listed above except for amphibians for which the only data were 17 records for predation by the mountain yellow-legged frog (*Rana muscosa*). The mean length of the predator was plotted against the mean length of the prey. The mean body lengths of both predator groups and prey consumed by each group were compared using one-way analysis of variance (ANOVA).

### 11.3.5. Diet composition

Data were collected from the literature on gut analyses of all nine predatory taxa. Diet preferences were recorded using a number of different methods which meant that interspecific comparisons had to be conducted in two batches. The first analysed those data that were collected according to the percentage of individuals with a given prey species in their faeces/gut (the "occurrence" method). The second analysis included those studies that recorded data according to the absolute number of each kind of prey item in the faeces/gut (the "number" method). Both analyses involved similar numbers of comparisons.

**Table 11.1 – Sources of data for diets of aquatic predators.**

| Group | Study | Species |
|---|---|---|
| Fish | Hynes (1950) *O+N* | *Anguilla anguilla, Salmo clarkii, Salmo gairdneri, Salmo salar, Salmo trutta* |
| | Hynes (1950) *O* | *Gasterosteus aculeatus, Pygosteus pungitius, Rutilus rutilus* |
| Amphibia | Griffiths (1986) *N* | *Triturus helveticus, Triturus vulgaris* |
| | Griffiths and Mylotte (1987) *N* | *Triturus vulgaris, Triturus cristatus* |
| Anisoptera (Odonata) | Blois (1985) *N* | *Aeshna cyanea, Anax imperator, Libellula depressa* |
| | Larson and House (1990) *O+N* | *Aeshna sitchensis, Cordulia shurtlefii, Leucorrhinia hudsonica, Libellula quadrimaculata, Somatochlora septentionalis* |
| | Pritchard (1964) *O* | *Aeshna canadensis, Aeshna eremita, Aeshna interrupta lineata, Aeshna juncea, Cordulia shurtlefii, Leucorrhinia borealis, Leucorrhinia hudsonica, Libellula quadrimaculata, Sympetrum spp.* |
| Zygoptera (Odonata) | Koperski (1998) *N* | *Enallagma cyathigerum* |
| | Larson and House (1990) *O+N* | *Enallagma cyathigerum* |
| | Lawton (1970) *N* | *Pyrrhosoma nymphula* |
| | Thompson (1978a) *N* | *Ischnura elegans* |
| Corixidae (Hemiptera) | Reynolds (1975)* *O* | *Cenocorixa bifida, Cenocorixa expleta, Hesperocorixa laevigata, Callicorixa audeni, Cymatia americana, Sigara spp.* |
| Notonectidae (Hemiptera) | Giller (1986)# *O* | *Notonecta glauca, Notonecta viridis* |
| Dytiscidae (Coleoptera) | Kehl and Dettner (2003) *O+N* | *Agabus nebulosus, Nebrioporus canaliculatus, Scarodytes halensis, Hygrotus confluens, Hydroglyphus geminus* |
| Hirudinea (Annelida) | Bradley and Reynolds (2006)* *N* | *Erpobdella octoculata, Helobdella stagnalis* |
| | Proctor and Young (1987)* *N* | *Alboglossiphonia heteroclite* |
| | Toman and Dall (1997) *N* | *Erpobdella octoculata* |
| | Young (1980)* *N* | *Helobdella stagnalis* |
| | Young (1981a)* *N* | *Erpobdella octoculata,* |
| | Young (1981b)* *N* | *Glossiphonia complanata* |
| Tricladida (Platyhelminthes) | Young (1981a)* *N* | *Polycelis nigra, Polycelis tenuis, Dugesia polychroa, Dendrocoelum lacteum* |

All data collected by examination of gut contents or faecal matter except: *=data collected by serological assay and #=data collected by electrophoresis. *O*=data collected using "occurrence" method, *N*=data collected according to "number" method.

Data were obtained either from tables in the publications cited in Table 11.1 or from analysis of figures. Taxonomic classification of prey was standardised to give the highest resolution possible without omitting any data. The resulting categories were (i) Annelida, (ii) Arachnidae, (iii) Mollusca, (iv) Chironomidae, (v) Cladocera, (vi) Coleoptera, (vii) Ephemeroptera and Odonata, (viii) higher Crustacea (Isopoda and Amphipoda), (ix) lower Crustacea (Ostracoda and Copepoda), (x) other Diptera, (xi) other Insecta, (xii) Vertebrata and (xiii) plant material. In the "number" analysis, this resolution was achieved simply by adding the constituent taxa together to form each of the categories. In the "occurrence" analysis the maximum percentage occurrence of the taxa within each classification was taken as an estimate of the proportion of the organisms containing that classification. Where values were recorded as "present" ("+") in occurrence data, it was assumed that only one individual contained this prey type and so the appropriate percentage was calculated from details in the text. In number data this was dealt with by assigning that prey classification a percentage of 0.1%.

Data included here used examination of gut contents/faeces, electrophoresis or serological analysis to investigate diet (see Table 11.1 for details). It was assumed that the absence of a report for a given category in gut/faeces analyses was indicative of that category not being included in the diet. The serological studies, however, targeted particular prey types *a priori* and so the same assumption could not be made. While the selection of target prey antigens was determined in all cases by laboratory trials in which the subject organism was offered a range of prey types, this is equivocal evidence for diet breadth. As such, I present two analyses, the first in which the serological analyses are excluded and the second in which they are included and non-reported categories of prey are assumed to be absent from the natural diet.

Variation in diet preference between groups of predators was assessed in each of the number and occurrence analyses using multivariate analysis of variance (MANOVA) with the taxon as the factor. Pillai's Trace was selected as the MANOVA statistic due to small sample sizes. The relatively small sample sizes meant that pair-wise comparisons between taxa were not possible. Instead, data were analysed using principal components analysis (PCA) and a visual analysis of plots of the first and second principal components were used to assess similarity between groups.

## 11.4. Results

### 11.4.1. Sensitivity to hydroperiod

The distribution of aquatic predators was significantly affected by water permanence in seven of nine groups (Figure 11.1). The exceptions were Dytiscidae, which occurred in almost all ponds, irrespective of the degree of water permanence ($\chi^2$=3.84, p=0.050) and Amphibia which occurred in fewer ponds but also showed no effect of hydroperiod ($\chi^2$=0.885, p=0.347). Corixidae, while being significantly reduced in non-permanent ponds compared to their occupancy of permanent ponds, still occurred in 72% of surveyed non-permanent ponds. Fish were substantially affected by hydroperiod and were found in only 10% of surveyed non-permanent ponds.

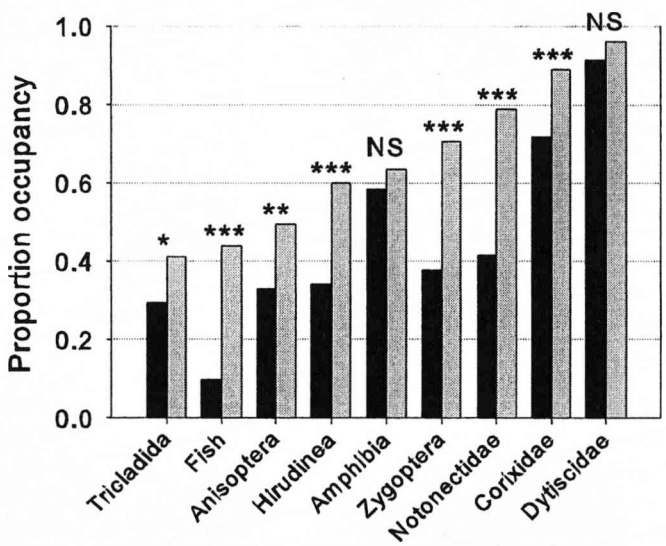


**Figure 11.1 – Proportion of 343 permanent (grey bars) and 106 non-permanent (black bars) ponds inhabited by aquatic predators in Cheshire, UK, and the result of a $\chi^2$ analysis to test for an association between the presence of each taxa and the degree of water permanence. ***=p<0.001, **=p<0.01, *=p<0.05, NS=not significant.**

### 11.4.2. Predators, permanence and aquatic macroinvertebrates

Water permanence and fish presence had a significant effect on family-level macroinvertebrate community structure (permutation test for ANOVA; hydroperiod: F=4.472, p<0.001; fish: F=8.003, p<0.001). Pairwise comparisons of predator-permanence treatment combinations showed that temporary fishless ponds and permanent fishless ponds differed in their macroinvertebrate communities but this was not significant after correction for six posthoc tests (Pillai's trace:

$F_{54,227}$=1.613, p=0.052). This is shown by the partial overlap of the 95% confidence ellipses in Figure 11.2. Permanent ponds varied depending on whether fish were present or not ($F_{60,274}$=3.289, p<0.001).

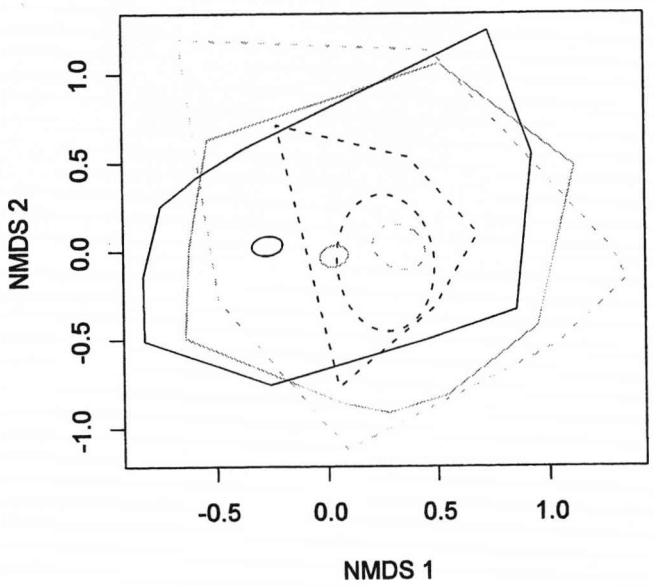


**Figure 11.2 – Nonmetric multidimensional scaling (NMDS) plot of family composition of macroinvertebrate communities in permanent (solid lines) and non-permanent (dashed lines) ponds either containing (black) or lacking (grey) fish. Ellipses are 95% confidence ellipses and polygons are convex hulls around points. Sample sizes are: permanent with fish = 145, non-permanent with fish = 9, permanent fishless = 190, non-permanent fishless = 92.**

Macroinvertebrate species richness was not significantly related to pond area but was significantly higher in permanent ponds compared to non-permanent ponds (area, $F_{1,436}$=0.450, p=0.504; permanence, $F_{1,436}$=58.6, p<0.001). Permanent ponds had on average 30.4 ±0.70 (SE) species whereas non-permanent ponds contained an average of 19.8 ±0.92 species.

Size distributions varied substantially among the predators ($F_{7,693}$=56.12, p<0.001, Figure 11.3), with comparable body sizes between invertebrates (mean 0.012m ± 0.0002 SE) but substantially larger body sizes in fish (mean 0.509m ±0.031 SE). The same variation was seen in the sizes of prey species ($F_{7,693}$=3.65, p=0.001, Figure 11.3). However, when records of predation by salmonids on other salmonids of length >0.8m were excluded from the dataset, prey size ranges were comparable ($F_{7,677}$=1.10, p=0.364).

Mollusca, including bivalves and gastropods, and Hirudinea were the largest of the freshwater macroinvertebrates, although the gastropod was a terrestrial species, *Deroceras laeve* (Pulmonata: Gastropoda). All these groups (length 0.15-0.20m) were larger than the sizes of prey recorded for invertebrate predators in the data collated by Brose et al. However, a substantial difference arises between these groups and the next largest invertebrate family, Hydrochidae (Coleoptera), at 0.06m (Figure 11.4). This body length is only within the range taken by fish and Dytiscidae. Apart from the Corixidae, all predator groups are capable of predating on the majority of macroinvertebrate families found in the pond surveys (Figure 11.5). Of the invertebrate predators, the Dytiscidae (97.2%) can handle the greatest proportion of prey families.

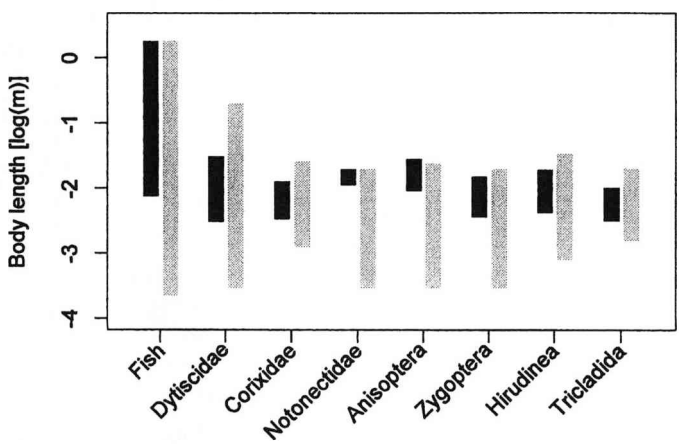


**Figure 11.3 – Comparison of predator body lengths (black bars) and body lengths of prey consumed by those predators (grey bars). Data from Brose et al. (2006).**

### 11.4.3. Taxonomic diet preferences

The taxonomic composition of the diet of aquatic predators included in this study varied significantly in both "number" analysis (all data: Pillai's trace; $F_{66,144}$=3.099, p<0.001, excluding serological and electrophoretic studies: Pillai's trace; $F_{55,70}$=3.310, p<0001) and both "occurrence" analyses (all data: Pillai's trace; $F_{55,105}$=3.007, p<0001; excluding serological and electrophoretic studies: Pillai's trace; $F_{33,39}$=2.159, p=0.011). A visual analysis of PCA plots suggests a strong similarity in diet between Hirudinea and Tricladida (Figure 11.6a), Anisoptera and Zygoptera (Figure 11.6a and b), Dytiscdae and fish (Figure 11.6c and d) and those latter two groups with Notonectidae (Figure 11.6a).

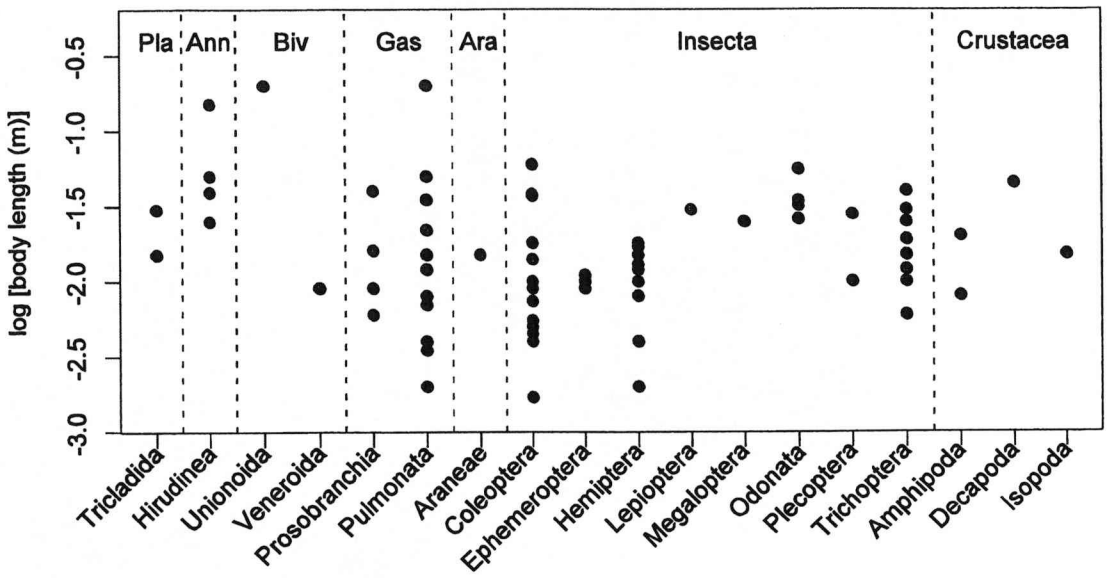


**Figure 11.4 – Maximum body lengths for families of macroinvertebrates in Cheshire ponds grouped by taxon. "Pla"=Platyhelminthes, "Ann"=Annelida, "Biv"=Bivalvia, "Gas"=Gastropoda, "Ara"=Arachnida.**

## 11.5. Discussion

As has been reported for other aquatic ecosystems, both the diversity and composition of macroinvertebrate communities in ponds in northwest England is strongly influenced by the presence of fish. However, fish are also the most susceptible to intermittent hydroperiods. For invertebrate prey species living in the ponds of north England, invertebrate predators appear to be capable of filling the predatory niche that may be left vacant as increases in temperature and a decline in hydroperiod make small aquatic ecosystems less suitable for fish. The evidence for only mild effects of environmental warming and fluctuating hydroperiod on macroinvertebrates is threefold: (i) little change in macroinvertebrate biomass under warming scenarios in mesocosm experiments (Feuchtmayr et al., 2007), (ii) the lack of statistical difference between communities inhabiting temporary and permanent fishless ponds and (iii) the absence of an effect of hydroperiod in at least one major invertebrate group. The Dytiscidae exhibit size and taxonomic preferences for the same invertebrate prey as fish and are found in a greater proportion of ponds with no preference between permanent and non-permanent water bodies. The relatively high proportion of invertebrate predator groups which appear susceptible to fluctuations in hydroperiod may be responsible for the relationship between the hydroperiod of temporary English ponds and the proportion of predators found therein (Bilton et al., 2001).

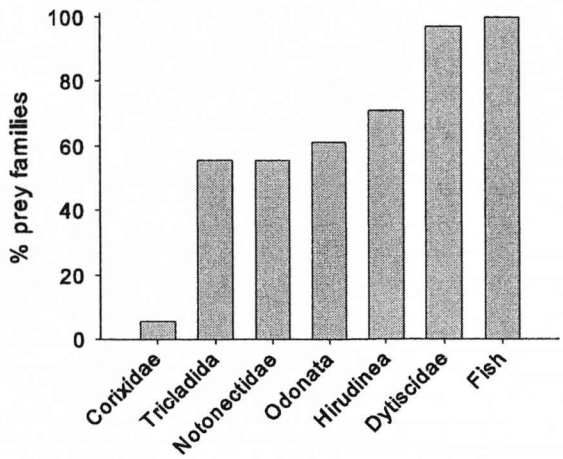


**Figure 11.5 – Percentage of macroinvertebrate prey families falling within the dietary limits of aquatic predator groups.**

The variation in prey species with hydroperiod-induced variation in predators has been illustrated for species of caddisflies (Trichoptera) (Wissinger et al., 2006). Vertebrate predators (salamanders) in permanent ponds were replaced by Dytiscidae in temporary ponds leading to communities of caddisflies which possessed traits adapted to dealing with the different predators. Our results demonstrate the ecological mechanisms (hydroperiodic and trophic) that could result in such a transition in English ponds. Similar species replacement patterns occur in damselflies under predation by either dragonflies or fish and in water bodies with different hydroperiods (Stoks and McPeek, 2003). However, it is important to note that such species replacements do not occur in all regions (Wissinger et al., 2009).

A complete transition from fish to fishless may not occur, even under extreme conditions. While many species of fish may not persist under changing aquatic conditions, there are some species for which hypoxia and high temperatures are less of a constraint. In the UK, *Carassius* spp. exhibit a high tolerance to hypoxia (Roesner et al., 2008), as well as damaging vegetation and causing increases in water turbulence (Richardson et al., 1995). However, these species are not currently widespread (Wheeler, 2000) and increases in distribution will rely on landscape-scale connectivity (Baber et al., 2002).

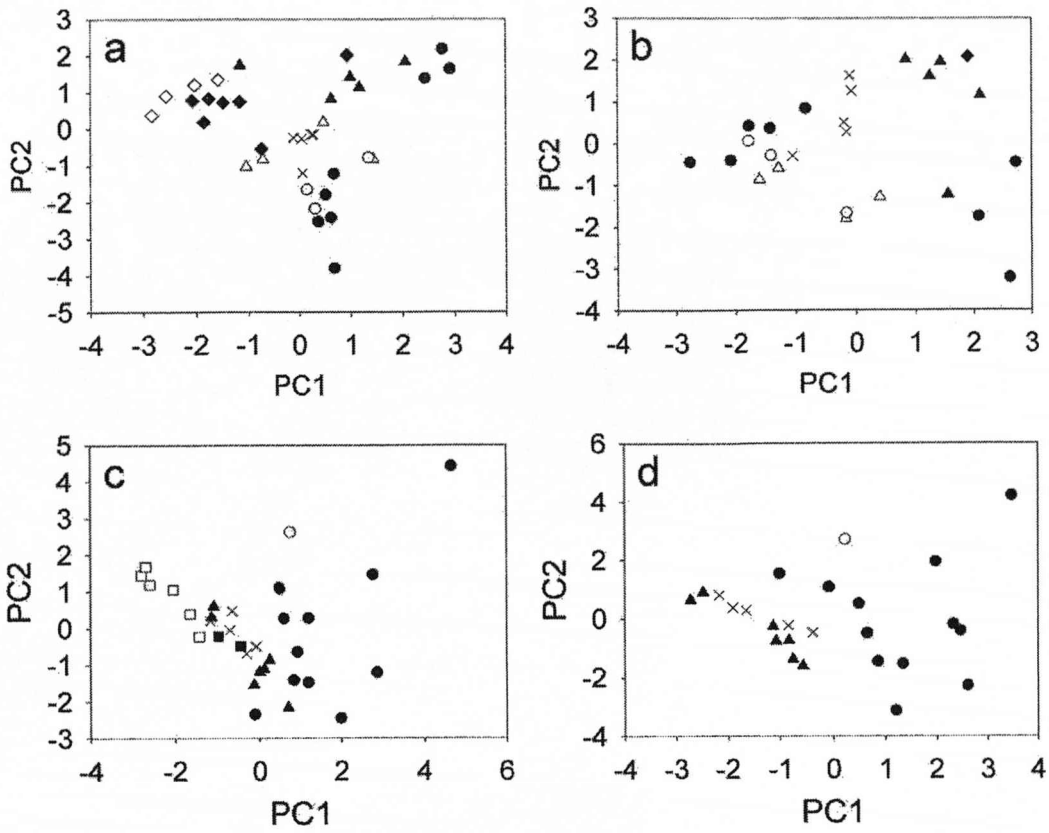


**Figure 11.6 – Comparison of the taxonomic composition of the diets of fish (▲) Amphibia (△), Anisoptera (●), Zygoptera (○), Dytiscidae (X), Notonectidae (□), Corixidae (■), Hirudinea (◆), and Tricladida (◇). The different plots relate to (a) the "numbers" method including serological and electrophoretic data, (b) the "numbers" method not including serological and electrophoretic data, (c) the "occurrence" method (*sensu* Hynes, 1950) including the serological and electrophoretic data and (d) the "occurrence" method not including the serological and electrophoretic data. First and second principal components explain 38.7% (Figure 11.6a), 39.3% (Figure 11.6b), 43.6% (Figure 11.6c) and 49.1% (Figure 11.6d) of the variance in the data.**

In an aquatic community with both vertebrate and invertebrate predation, it has been shown that even a small (approximately 0.8-1.1mm body length (Morton, 1985)) invertebrate predator (*Cyclops bicuspidatus* (Crustacea: Copepoda)) can exert a greater grazing pressure on aquatic zooplankton than the main fish species (*Osmerus mordax* (Actinopterygii)) (Lane, 1979). Recent work has shown that *Daphnia* populations can be regulated by a combination of vertebrates (coregonid spp. (Actinopterygii)) and invertebrates (*Leptodora kindtii* and *Bythotrephes longimanus* (Crustacea: Cladocera)) but that the invertebrate had the greatest impact during the summer (Manca et al., 2008). The comparable intensity of predatory interactions between invertebrate (*Erpobdella*

*octoculata* (Annelida: Hirundinea)) and vertebrate (*Salmo trutta* (Actinopterygii)) predators has also been shown in lotic freshwater habitats (Dahl, 1998).

Dahl (1998) also demonstrated that the invertebrate predator selected smaller prey while the vertebrate predator selected larger prey. The presence of ontogenetic size refugia for prey species has a more substantial impact on smaller invertebrate predators than on larger vertebrate predators. This result has also been found for *Daphnia* predated in natural systems (Manca et al., 2008) and experimental mesocosms (Hanazato and Yasuno, 1989). The combination of variation in selection pressure due to predators along with the selection pressures of different degrees of water permanence is thought to generate observed patterns in aquatic community structure (Wellborn et al., 1996). The complexity of invertebrate-vertebrate predator interactions has been highlighted by attempts to predict the combined functional responses of invertebrate (*Agnetina capitata* (Plecoptera: Perlidae)) and vertebrate (*Cottus bairdi* (Actinopterygii)) predators. Observed functional responses deviate from those predicted from the functional responses of the two predators individually (Soluk, 1993). The size distribution of potential prey for invertebrates may resemble that of fish, but the actual size distribution of individuals that are preyed upon varies according to size of the predator and handling time. The species-averaging of predator : prey body size ratios has been criticised for underestimating the true difference in size between predator and prey on an individual level by up to an order of magnitude (Woodward and Warren, 2007).

A protracted transitional period in freshwater communities resulting from a high rate of climate-induced extinction and a low rate of colonisation by warm-adapted species means that the stable temporary communities observed in other regions will take time to establish. The plight of freshwater ecosystems on islands, such as those in the UK, is complicated by the lack of immigration by warm-water taxa from the south. This makes less dispersive elements of the UK aquatic fauna and flora candidates for assisted colonisation (Hoegh-Guldberg et al., 2008). More research is needed into the implications for the introduction of fish from continental Europe into UK water bodies.

Acidification has a range of biological implications (Stenson and Eriksson, 1989) including the extinction of fish populations in both lentic (Beamish and Harvey, 1972, Henrikson et al., 1989) and lotic (Olofsson et al., 1995) aquatic systems. Macroinvertebrate communities in fishless lakes have been shown to be less sensitive to pH than fish (Bendell and McNicol, 1987, Bradt and Berg, 1987). Acidification therefore results in the replacement of fish with invertebrate predators but lacks the

additional stress of hydroperiodic reduction. Taxa shown to benefit from this change include Odonata (Nilsson, 1981, Henrikson, 1988) and Corixidae (Henrikson and Oscarson, 1981). The latter group became top predator in the studied system. Variation between macroinvertebrate communities in water bodies where fish have been lost due to hydrological or thermal pressure and due to acidification merits attention.

## 11.6. Conclusions

Changing environmental conditions will create a state of flux in which currently-permanent water bodies go through hydroperiodic and thermal transitions. These transitions will alter community structure through species replacement, particularly in the case of fish, in response to changes in abiotic selection pressures as well as the changes in biotic selection pressures that result from them. Aquatic invertebrate predators (particularly Dytiscidae, as highlighted in previous studies (Wissinger et al., 2006)) are less susceptible to variations in hydroperiod and increases in environmental temperature than fish while occupying approximately the same trophic niche. The results of this study suggest that, while there is a high degree of trophic overlap between vertebrate and invertebrate predators which may buffer the *ecological* transition, there will still be substantial changes in patterns of predation which will alter *evolutionary* pressures.

# *Chapter 12. Conclusions*

## 12.1. Summary of key findings

While a large number of studies and their results are discussed in this thesis, there are a number that warrant particular mention due to their relevance to the broader scientific community:

- *Aquatic taxa exhibit similar phenological shifts to terrestrial taxa*

  While a large number of reports of changing phenology have been described in the literature, Chapter 3 represents the first description of such a response in an aquatic taxon. Due to the uncertain nature of the relationship between terrestrial and aquatic temperature variation, this was not a trivial finding. This result adds to the consensus in the signal of advancing phenology and, hence, to the broader evidence for directional climate change.

- *Range shifts affect water quality metrics*

  The inclusion of a wide number of insect taxa in metrics that are used to assess water quality involves the assumption that water quality alone determines the distributions of those taxa. I demonstrate the effect that range shifts have on assessments of water quality, principally the increase in species richness from a small number of cold-hardy, eurytopic species with relatively low BMWP scores to a more diverse community which also contains species with higher BMWP scores. This must be addressed in re-evaluations of the RIVPACS baseline comparison.

- *Current estimates of range shifts are flawed*

  In an evaluation of methods that have been used to detect shifts in range from historical records, those used in the analysis of odonate data were found to be unreliable. An alternative calculation is presented with methods that are shown to reliably control for recorder effort.

- *Climatic effects on immune function may restrict odonate distributions*

  While bioclimate envelope models have been used to describe and predict the geographical ranges of species under climate change, the underlying physiological processes that contribute to these range limits are largely uninvestigated. In a small number of studies the effects of bioclimatic variables on survival have been examined (Crozier, 2004a, e.g. Crozier, 2003, Crozier, 2004b). However, studies on the proximate causes of mortality are still rarer. I provide some preliminary evidence that immune function may vary across the geographic range to the point at

which the trait that gives the "banded demoiselle" its vernacular name ceases to be a "band" but instead better resembles a "spot".

- *Botanical communities are the most significant predictors of odonate community structure*

  A large number of factors have been implicated in the determination of the composition of odonate assemblages. I demonstrate that it is the structure of the botanical communities of ponds of northwest England, and to a lesser extent hydrogeological properties of the water body, that govern the structure of odonate communities. In addition I provide the first test – and refutation – of the suggestion that plant species can act as indicators of the nature of the water body that Odonata can use in selecting oviposition sites. An understanding of the habitat requirements of Odonata is vital in understanding odonate metapopulation dynamics. This theory then feeds into knowledge concerning the permeability of the landscape that Odonata must be able to pass through in order to shift their ranges in response to environmental warming.

- *Odonata in isolation are not reliable indicators of general species richness*

  The reliance of Odonata on unpolluted water bodies, as reflected in their relatively high BMWP scores, makes them a potential candidate indicator of high biodiversity in the wider biological community. While this is borne out in a general sense with significant correlations between odonate species richness and the species richness of plants and macroinvertebrates, the explanatory power of odonate richness is very low. This suggests that, while the inclusion of Odonata in more complex metrics may be warranted, their use in isolation is unwise.

- *Dytiscidae will become dominant predators in the UK's small water bodies as they enter hydroperiodic transition*

  There has been considerable interest in the ecology of temporary waters and the deviation from the community structure found in permanent water bodies that drying out entails. This has resulted in descriptive and experimental work investigating the particular adaptations that temporary water species have acquired to persist in this harsh environment. I provide a theoretical underpinning to explain why one might expect transitions between different members of one section of the aquatic biota, the predator community, under decreasing hydroperiod and assess the ramifications for the foodweb from such transitions. I demonstrate that vertebrate predators such as fish are most likely to be succeeded by the Dysticidae (Coleoptera) as small water bodies enter hydroperiodic flux. Furthermore, an analysis of the

dietary preferences of dytiscid beetles shows that they consume approximately the same prey both in terms of taxonomic composition of the diet and the range of prey sizes that they are capable of handling. The results of this study are supported by the observation that Dytiscidae take over from vertebrate predators (salamanders) along a pond permanence gradient in Spain (Wissinger et al., 2006).

Taken together, these results suggest that the British Odonata will generally increase in abundance and geographic range in the near future. The species-poor regions of northern Scotland will be rapidly colonised over the coming decade by species that reach a range margin in central or northern England. That range expansion may be caused by factors such as an alleviation of thermal pressures on immunology and dispersal. The expanding species are likely to have populations containing larger individuals at the range margin. The ecological implications for a sudden invasion by relatively large-bodied individuals of newly-arrived species of Odonata into naive ecosystems are not clear. The rarity of species with northern distributions in the UK does not provide sufficient data to permit an assessment of their conservation status in the face of climate change. Despite being better adapted for life in an aquatic landscape that is in hydroperiodic flux, the Odonata are not predicted to dominate the predatory niche as vertebrate predators become rarer.

## 12.2. Positive (regional) aspects of climate change

I have heard it said that the impacts of climate change are "not all bad". In fact, several times I have heard people offer the view that in their particular field climate change is a *good* thing. In the case of Odonata, it might be tempting to take the reported range shifts and resultant increases in diversity as evidence for a beneficial effect of climate change. Indeed this is the case on a regional level. Species richness increases with temperature and the expansion of European continental species into the UK is likely to substantially augment the numbers of species occurring in a given site over the coming years.

However, it is vital to emphasise that the range shifts that are occurring are *whole-range shifts* and not range *expansions*. In the northern hemisphere a poleward expansion of the northern range margin is accompanied by a retraction at the equatorward range margin. Eventually this would be predicted to lead to a reduction in the number of species persisting at the equator resulting in two peaks of species richness at a certain latitude above and below the equator.

## 12.3. Role of Odonata in climate change research

As I write this chapter I await the imminent publication of two books which highlight the importance of Odonata to research on climate change. One, edited by Jürgen Ott and entitled *Monitoring Climate Changes with Dragonflies*, brought together a collection of studies highlighting the effects of climate change on the order (Ott, 2008). While largely confined to documenting distributional changes across a variety of global regions (8 of 15 chapters), topics including diversity, anthropogenic effects, extreme weather events, dispersal and population dynamics are also included. The second book describes the general utility of Odonata as model organisms in ecology and evolution in a collection of work edited by Alex Cordoba-Aguilar (2008). I also cover the positive aspects of Odonata for use in research in Chapter 2.

## 12.4. Distributional changes

As illustrated by the imbalance of content in Jurgen Ott's recent book, distributional changes dominate the world of climate research. Such range shifts are relatively easy to describe based on field observations and anecdotal or historical records. However, as I point out in Chapter 4, the zeal with which such studies are pursued may result in the application of inappropriate methods. There are many other potential problems with such studies, primarily in the lack of records explicitly confirming the absence of a species in a given area. However, the establishment of standardised monitoring schemes has only been successful in the cases of birds (e.g. the UK Breeding Bird Survey), butterflies (Butterfly Monitoring Scheme), and aphids (through the suction trap network which began in the UK under the Rothamstead Insect Survey and the Scottish Agricultural Science Agency and is now implemented across Europe). While Odonata are currently missing from that list, the methods used in the Butterfly Monitoring Scheme ("Pollard walks") provide a blueprint for the kind of techniques that could be used for monitoring adult odonate populations.

## 12.5. Availability of historical records

However, this is not to say that baseline data do not exist. In the UK the Environment Agency has a well-established river monitoring network looking at the biological communities of 6,000 river sites monitored every six months. While these data are valuable in assessing water quality, they also give a baseline dataset for the investigation of distributional trends in lotic fauna. While similar datasets do not occur for lentic water bodies, there are instances where data may be available. These include the PondLIFE dataset described in Chapter 10 and the National Ponds Database currently held by Pond Conservation.

The recent rise in popularity of phenology (such as the study described in Chapter 3) is partly due to the historical records which were collated from a range of obscure sources. It is often remarked that the number of historical biological records is often proportional to the density of vicars, who constituted a particularly meticulous group of biological recorders. It is likely that other such data sources could provide similar baseline data and these should be explored, no matter how unusual the source.

With the fairly substantial data that we do have on the distributions of Odonata over the past century, the next task is to generate a European database to collate these data. Such a continent-wide approach would permit the parameterisation of climate space models to assess which aspects of climate influence the distributions of Odonata. However, until this spatial scale of detailed mapping is available, parameterisation will remain imprecise.

Detailed knowledge of where organisms occur can be used to target field and laboratory studies aimed at identifying proximal physiological causes of range margins. Examples are given in Section 2 of this thesis, including dispersal morphology (Chapters 6 and 8), immunology (Chapter 7) and wing morphology (Chapter 9). This is an important next step in research into climate change and Odonata, since little investigation has been carried out into which biological traits are influenced by climate change, to what extent, and the relative importance of those effects.

## 12.6. Climate change and the aquatic environment

If Odonata are all responding to broadly the same climate signal, that of increasing environmental temperature, then it might be expected that all species would be tracking climate change at the same rate. The lag exhibited by range shifts relative to rates of climate space expansion highlights the need for the continued monitoring of habitat connectivity and the identification and preservation of existing bodies of water that provide pristine refugia in anthropogenically altered aquatic landscapes. A further consequence of climate change that has not been considered in terms of the impacts on Odonata is the inevitable transition of some water bodies from permanent to temporary or the complete loss of those water bodies. Hydrological models describing the prognosis for a given range of water bodies would aid in the prediction of future landscape connectivity. Such models exist for fairly basic temporary water bodies such as rock pools but are lacking for more common ponds and lakes.

However, as with all matters having the potential to be affected by climate change, alternative hypotheses must also be included. It is commonly believed today that one of the implications of climate change is a spread of malaria to temperate regions. As mentioned briefly in Chapter 1, the spread of tropical diseases is inhibited or promoted by a range of factors of which climate is but one. It was the draining of large areas of marsh and fen that removed the breeding habitat for the British malaria vector several hundred years ago, not a change in climate. Just as man removed the mosquito's breeding habitat, so has he also, purposely or not, removed a large amount of habitat for Odonata and the destruction continues to this day. However, the context within which the damage is done can vary in the level of malice from the simple, wanton vandalism perpetrated by those who actively pollute water bodies to less direct forms of damage such as changes in farming practices. For example, the recent change in the Common Agricultural Policy that shifted subsidies from being linked to productivity to being linked to environmental awareness may result in reduced herd size for livestock which, in turn, results in a lower grazing pressure and, finally, increased plant growth with increased rates of succession and increased natural water abstraction from those larger plants.

Dispersal data are still lacking for most odonates and the data that have been reported have only limited use. However, recent technological advances may enable a greater precision in dispersal monitoring through the use of electronic tags. This has already been made use of in a fascinating study on *Anax junius*, the common green darner, where the insects were tracked by plane using radar telemetry (Wikelski et al., 2006). *Anax junius* is of comparable size to the largest of the British Odonata, making the methods of Wikelski and colleagues applicable in study of the UK odonate fauna. Initial studies suggest that a similar approach might be possible with Libellulidae on a smaller scale (Hardersen, 2007). The size differences of *Anax junius* and *Libellula fulva* (the latter species being that used in the study by Hardersen) are shown in Figure 12.1 in relation to British species. Researchers at Rothamstead Research having already tracked bees (Riley et al., 1996) and butterflies (Cant et al., 2005) using harmonic radar, a method that could be applied to Odonata.

Alternative methods for relative comparisons of odonate dispersal distances are the laboratory approaches of Marden (1987) and Simmons and Thomas (2004). Each method would provide interesting flight-related data. The former method would provide an opportunity to compare lift generation in "perchers" and "fliers" within and between families. The latter method would provide data on dispersal distances which could complement data from mark-release-recapture studies.

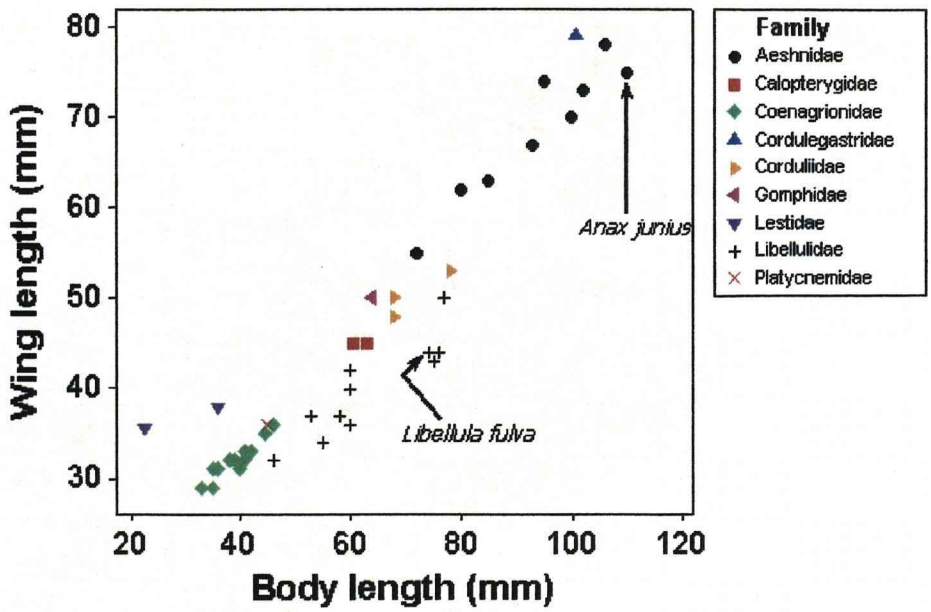


**Figure 12.1 – Body size variation in British odonates in relation to those species which have been used previously in telemetry experiments (*Libellula fulva* and *Anax junius*).**

## 12.7. Odonata in changing aquatic communities

I have shown that a range of invertebrate predators, particularly the Dytiscidae, exhibit dietary preference that overlap with those of fish to varying degrees. A next step in this area would require experimental work to determine the functional responses of invertebrate and vertebrate predators to a range of prey species using standardised methods. Predatory species should be tested in isolation with each prey species to ascertain comparable functional responses and then tested in combination to investigate the effects of interference and competition.

In addition to the varying extinction risk of different taxa within aquatic ecosystems, the impacts of invading species have not been examined. A particular case is that of *Erythromma viridulum*, which has been breeding in south-east England since 2002. There is a possibility that an invasion by a new species of predator will affect community structures in habitats where it has become established. As with distributional data, there is a need for a baseline in order to properly assess the results of invasion. Such baseline data might be present in the biological records of the National Pond Database, as mentioned above.

## 12.8. Aquatic ecosystem services and conservation

For many years freshwater scientists have attempted to overcome the negative press that wetlands have received. This includes natural associations with flies, mosquitoes and bad odours and the risks to health such as tales of men being swallowed alive by bogs in Richard D. Blackmore's novel, *Lorna Doone*. Standing water bodies have acted as "sinks for the consequences of human activity" (Moss, 1998) for many years, resulting in a poor public image that is reinforcing this neglect.

It is estimated that there are around 400,000 ponds in the United Kingdom representing 97% of all standing freshwater bodies. However, long-term declines in pond numbers has been estimated to be around 1% per annum (Haines-Young et al., 2000) with substantial loss occurring since the Second World War (Barr et al., 1994). The major sources of loss have been identified as changing agricultural practices, urban sprawl and "benign neglect" (Boothby and Hull, 1999). However, aside from the purely biological reasons for the conservation of aquatic communities, there are also arguments for conservation stemming from the "ecosystem services" (natural processes that enhance the quality of human life) that they provide. These can be categorised into four groups:

### 12.8.1. Preventing floods and storing water

Some schemes have been set up to control the flow of surface water resulting from heavy rains in an attempt to mitigate flooding (so-called "downstream flood storage areas"). However, there is a growing consensus that strategic pond networks can be used to greater effect. A number of experimental sites are investigating this potential application.

### 12.8.2. Reducing diffuse pollution

Ponds are capable of substantially reducing the phosphorus (by up to 50%) and nitrogen (up to 20%) concentrations of surface water (Hawkins and Schofield, 2003). Compounds of these two elements, which are used in agriculture as fertilisers, constitute a major source of water pollution. Such reductions in pollutants can be achieved while the ponds themselves retain either "moderate" or "good" water quality ratings under the EU Water Framework Directive.

### 12.8.3. Mitigating climate change effects

Recent studies have shown that agricultural ponds sequester vastly more carbon than any other type of biotope (Table 12.1, Downing et al., 2008). Estimates of the number of ponds suggest that this type of water body may sequester almost four times the amount of carbon as all of the world's oceans. Their relative ease of creation makes ponds a preferable alternative to other mitigation measures.

Table 12.1 – Rates of carbon sequestration in different land use types.

| Biotope | Carbon sequestration (grams carbon $m^{-2}$ $yr^{-1}$) |
|---|---|
| Ponds | Up to 5,000 |
| Forest biomass | Up to 400 |
| Lakes | Up to 15 |
| Forest soils | Up to 12 |

### 12.8.4. Increasing agricultural productivity

Along with other landscape elements, ponds provide a habitat that increases biodiversity and there is growing evidence that this biodiversity enhances agricultural outputs (e.g. Altieri, 1999). The Countryside Stewardship Scheme (1991-2005) and its successor, Environmental Stewardship (2005-present) have gone some way towards providing an economic incentive for the conservation of landscape elements such as ponds within the UK's agricultural landscape. A "no net loss" approach to pond loss (Boothby, 1997) combined with a program of pond creation has led to an increase in the number of ponds over recent years, although the rate of loss of existing ponds has continued unabated (Haines-Young et al., 2000). The current preparation of a new Habitat Action Plan (HAP) specifically aimed at protecting this valuable resource has broadened freshwater conservation measures to include more than simply the larger lakes.

Ponds represent an increasingly important (though neglected) natural resource due to their potential ability to mitigate flooding, water pollution and climate change, as well as their relatively high biodiversity. Further study is needed into the ways in which strategic networks of small water bodies can be created and used to exploit biological and hydrogeochemical processes to enhance the ecosystem services that are already provided. Only by further study will we be able to fully appreciate the substantial economic value of this resource. With government bodies looking for economic returns from investment in scientific research, the clear potential economic value of ponds may give a firm foothold in funding proposals.

## 12.9. Final thoughts

It is impossible to ignore the presence of a group of organisms so biologically fascinating and aesthetically striking as the Odonata. This has resulted in their inclusion within the folklore of cultures wherever they occur, although different traditions are divided over whether they represent good or evil. In the East dragonflies are revered as beautiful, noble creatures. So strong is this

sentiment that the dragonfly became a national symbol of Japan. After a 7th century Japanese emperor observed a dragonfly killing a gadfly by which he had just been bitten, a haiku was written which renamed central Japan *Akitsu-shima* ("Land of the Dragonflies") in honour of the creature. Dragonflies feature widely in eastern medicine, art, poetry (particularly haiku) and even cuisine, where they traditionally feature as a staple part of the Balinese diet when other food sources are rare.

The West, on the other hand, has been far more suspicious of the dragonfly. This is immediately evident in some of the colloquial names for the insects: "horse stinger" (UK and Australia), "devil's darning needle" (USA), "troll's spindle" (Sweden) and "eye poker" (Norway). The various legends which give rise to these monikers involve a range of fallacious "old wives tales". The Native Americans are alone among western peoples in considering the dragonfly to be a positive entity, associating it with renewal, swiftness and purity of water.

Interestingly, this final belief in the dragonfly as an indicator of water quality has been confirmed and exploited by modern environmental science. Studies of mankind's effects on freshwaters have revealed that the dragonfly and damselflies are particularly sensitive to these impacts, making them ideal "ecological indicators". Indeed, the monitoring of river quality in Europe involves a survey of the invertebrate communities, including a range of dragonfly species, inhabiting those bodies of water in order to make inferences about the state of the river.

For all the distrust of dragonflies in the west, there is no doubt that they perform valuable ecological services. Among other tasks in the ecosystem, dragonflies consume vectors of disease, such as mosquitoes, as well as preying on biting and stinging insects, throughout both the aquatic and terrestrial stages of their life cycles. They, in turn, provide a major food source for fish, thus forming a link between the smaller invertebrates in aquatic systems and the larger vertebrate predators.

The earliest fossil Odonata have been found in sediments from the Lower Permian which date back 250 million years. It has been proposed that groups of organisms such as the Odonata that have such extensive and ostensibly stable evolutionary histories should be resilient to modern global change. Evolutionary time can be likened to a hurdles race: the Odonata have persisted through many trials and tribulations, including four major extinction events (one of which claimed the dinosaurs) and countless less severe oscillations of climate and geology. Each of these represents a hurdle over which an organism must leap to survive. However, clearing each hurdle requires certain

adaptations and those adaptations will be inherited by successive generations of that species, enabling it to clear similar hurdles in the future. By this reasoning, the modern Odonata should possess a battery of adaptations that leaves them prepared for almost anything Nature could throw at them.

Unfortunately it is at this point where the tale becomes less positive for, although the Odonata are extremely flexible in terms of adapting to changes in environmental conditions, there is evidence that the modern phase of climate change is unprecedented in their evolutionary history. This, therefore, represents a new hurdle which some or all of the Odonata may fail to clear. Added to this is the synergistic impact of other detrimental, anthropogenic factors such as the pollution of water bodies, the draining of marshes and fens and even the well-intentioned (though ultimately destructive) "amelioration" of water bodies through dredging and introduction of damaging plant and fish species. Thus, while humans have a tendency to view dragonflies in a negative light, it is in fact the dragonflies that suffer from their interaction with man.

With popular naturalism beginning to show a greater appreciation for the invertebrate world as well as the more traditional cute and cuddly vertebrates, we can only hope that the public will be inspired to help in the conservation of these creatures. For surely there can be few groups of organisms more appropriate as flagship species for the conservation of our wetlands than the dragonflies.

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## *Glossary*

| Term | Definition |
|---|---|
| *Aestivation* | A period of metabolic stasis brought on my high temperatures and dessication. |
| *Aspect ratio* | A measure of the shape of wings calculated as wingspan$^2$/wing area. A high wing aspect ratio indicates long, thin wings and is characteristic of high dispersal ability. |
| *Bioclimate envelope model* | Models of species distributions based on the premise that climatic variables alone influence where a species can persist. |
| *Diapause* | Developmental stasis which, in Odonata, can be brought about by low temperatures, photoperiod or dessication. |
| *Ellenberg values* | Values attributed to plant species according to their indicative value for particular habitat characteristics. These include "continentality" (K), "moisture" (F), "light" (L), "soil reaction" (R) and "fertility" (N). |
| *Episodic drying* | Predictable drying of a water body. |
| *Flight period* | The temporal range over which a species is found in the adult form. |
| *Fluctuating asymmetry* | The deviation from symmetry in paired phenotypic traits. |
| *Functional response* | The pattern of prey consumption at varying prey densities. |
| *Fundamental niche* | The range of values of abiotic factors that an organism is capable of surviving. |
| *Geometric morphometrics* | A mathematical technique used to investigate variations in shape using landmarks as a multivariate dataset. |
| *Harmonic radar* | A device used to monitor the location of small insects in dispersal experiments. The radar emits radiowaves which are reflected back at a difference frequency from small antennae attached to individual insects allowing their locations to be determined in real time. |
| *Hydroperiod* | The pattern of variation in water level within a water body. |
| *Intermittent drying* | Unpredictable drying of a water body. |
| *Katatrepsis* | The rotation of the embryo in invertebrate eggs. |
| *Landmark* | A point on an image that is defined in terms of its cartesian coordinates, which are then used as multivariate data in geometric morphometrics. |
| *Mark-release-recapture (MRR)* | A technique whereby population sizes can be estimated by capturing, marking and releasing individuals and then assessing the relative capture frequencies of marked and unmarked individuals. Where individual marks are used the movements of individual animals can be measured, hence the use of the technique in dispersal studies. |

| | |
|---|---|
| *Melanotic encapsulation* | The process in the invertebrate immune response whereby foreign objects in the haemolymph are engulfed by melanised haemocytes. |
| *Multivoltine* | Passing through three or more generations in a single year. |
| *Node* | The intersection of wing veins. |
| *Obelisking* | A thermoregulatory behaviour exhibited by Odonata in which the tip of the abdomen is pointed towards the sun in order to minimise the surface area of the body that is exposed to insolant radiation. |
| *Ordinal date* | The number of days since 1st January. |
| *Parthenogenesis* | Asexual reproduction whereby females produce viable, female offspring without mating. |
| *Partivoltine* | Requiring three or more years to pass through a single generation. |
| *Phenology* | The timing of life history events (and the study thereof). |
| *Photoperiod* | The variation in day length. |
| *Pleistocene megafauna* | The collective term for the large-bodied vertebrates that dominated the Pleistocene but went extinct shortly after. |
| *Procrustes transformation* | A technique used in geometric morphometrics to control for variations in size and rotation of images. This allows only the variations in shape to be compared. |
| *Quaternary period* | The geological period lasting from 2.588 million years ago to the present. This includes both the Pleistocene (2.588mya - 0.0117mya) and Holocene (0.0117mya - present) epochs. |
| *Semivoltine* | Requiring two years to pass through a single generation. |
| *Spring species* | Species which possess a diapause in the final larval instar in which they spend the winter before emergence. After winter these species proceed rapidly to a synchronised emergence early in the summer. |
| *Summer species* | Species lacking a diapause in the final larval stage. These species emerge later in the season and lack synchronicity. |
| *Trophic cascade* | The knock-on effect produced by variations in the abundance of organisms at a particular trophic level on the abundances of organisms not only on the neighbouring trophic levels but also, through those neighbouring trophic levels, throughout the foodweb. |
| *Trophic decoupling* | A phenomen by which variations in phenology lead to predators and their prey becoming separated in time so that the interaction no longer occurs. |
| *Turlough* | A pool on exposed limestone exhibiting seasonal drying patterns. There is only one example of this water body in Wales and all others are found in Ireland. |

| | |
|---|---|
| *Univoltine* | Passing through a single generation in a year. |
| *Vernal pond* | A small water body which is created by snowmelt and spring rains but dries up during the summer. |
| *Voltinism* | The number of generations an individual is capable of passing through in a single year. |
| *Wing loading* | The amount of body mass that is lifted per unit area of wing. |
| *Winter critical size* | According to Norling (1984), the winter critical size is a developmental threshold which must be reached in order for the individual to continue development in the next year. Where the threshold is not reached the individual enters development stasis (diapause). |

## *Appendix – Abbreviations*

| Abbreviation | Definition |
|---|---|
| AIC | Akaike's Information Criterion |
| ANCOVA | Analysis of Covariance |
| ANOVA | Analysis of Variance |
| ASPT | Average Score Per Taxon |
| BDS | British Dragonfly Society |
| BMWP | Biological Monitoring Working Group |
| BOD | Biological Oxygen Demand |
| CCA | Canonical Correspondance Analysis |
| CET | Central England Temperature |
| COD | Chemical Oxygen Demand |
| CSM | Common Squares Method (in Chapter 4) |
| CVA | Canonical Variates Analysis |
| DAFOR | Dominant, Abundant, Frequent, Occasional, Rare |
| DPA | Diel Patterns of Activity |
| ENSO | El Nino - Southern Oscillation |
| FA | Fluctuating Asymmetry |
| GLM | General Linear Model |
| IPCC | Intergovernmental Panel on Climate Change |
| IUCN | International Union for Conservation of Nature |
| LTT | Lower Thermal Threshold |
| MANOVA | Multivariate Analysis of Variance |
| MRR | Mark-Release-Recapture |
| NAO | North Atlantic Oscillation |
| NCM | No Control Method (in Chapter 4) |
| NMDS | Non-metric Multidimensional Scaling |
| PAST | Paleontological Statistics |
| PCA | Principal Components Analysis |
| pCCA | Partially Constrained Correspondance Analysis |
| PSYM | Predictive System for Multimetrics |
| RFW | Right forewing |
| RIM | Regression Intercept Method (in Chapter 4) |
| RIVPACS | River Invertebrate Prediction, Assessment and Classification System |
| RM | Resampling Method (in Chapter 4) |
| SAC | Special Area for Conservation |
| SSSI | Site of Special Scientific Interest |
| T:A ratio | Thorax : abdomen ratio |
| $TD_{10}$ | Threshold Density 10% (in Chapter 4) |
| $TD_{25}$ | Threshold Density 25% (in Chapter 4) |
| WCS | Winter Critical Size |
| WL:AL | Wing loading : abdomen length |

## *Appendix – Taxonomic authorities for Odonata*

| Species | Authority |
|---|---|
| *Aeshna caerulea* | Ström, 1783 |
| *Aeshna canadensis* | Walker, 1908 |
| *Aeshna cyanea* | Müller, 1764 |
| *Aeshna eremita* | Scudder, 1866 |
| *Aeshna grandis* | Linnaeus, 1758 |
| *Aeshna interrupta lineata* | Walker, 1908 |
| *Aeshna isosceles* | Müller, 1767 |
| *Aeshna juncea* | Linnaeus, 1758 |
| *Aeshna mixta* | Latreille, 1805 |
| *Aeshna sitchensis* | Hagen, 1861 |
| *Anax imperator* | Leach, 1815 |
| *Anax junius* | Drury, 1773 |
| *Argia vivida* | Hagen in Selys, 1865 |
| *Brachytron pratense* | Müller, 1764 |
| *Calopteryx maculata* | Palisot de Beauvois, 1805 |
| *Calopteryx splendens* | Harris, 1776 |
| *Calopteryx virgo* | Linnaeus, 1758 |
| *Ceriagrion tenellum* | de Villers, 1789 |
| *Coenagrion armatum* | Charpentier, 1840 |
| *Coenagrion hastulatum* | Charpentier, 1825 |
| *Coenagrion mercuriale* | Charpentier, 1840 |
| *Coenagrion puella* | Linnaeus, 1758 |
| *Coenagrion pulchellum* | Vander Linden, 1823 |
| *Coenagrion scitulum* | Rambur, 1842 |
| *Cordulegaster boltonii* | Donovan, 1807 |
| *Cordulia aenea* | Linnaeus, 1758 |
| *Cordulia shurtlefii* | Scudder, 1866 |
| *Enallagma aspersum* | Hagen, 1861 |
| *Enallagma cyathigerum* | Charpentier, 1840 |
| *Enallagma hageni* | Walsh, 1863 |
| *Erythromma najas* | Hansemann, 1823 |
| *Erythromma viridulum* | Charpentier, 1840 |
| *Gomphus vulgatissimus* | Linnaeus, 1758 |
| *Ischnura elegans* | Vander Linden, 1820 |
| *Ischnura hastata* | Say, 1839 |
| *Ischnura pumilio* | Charpentier, 1825 |
| *Lestes congener* | Hagen, 1861 |
| *Lestes dryas* | Kirby, 1890 |
| *Lestes forcipatus* | Rambur, 1842 |
| *Lestes sponsa* | Hansemann, 1823 |
| *Lestes viridis* | Vander Linden, 1825 |
| *Leucorrhinia borealis* | Hagen, 1890 |

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| *Leucorrhinia dubia* | Vander Linden, 1825 |
| *Leucorrhinia hudsonica* | Selys, 1850 |
| *Libellula depressa* | Linnaeus, 1758 |
| *Libellula fulva* | Müller, 1764 |
| *Libellula quadrimaculata* | Linnaeus, 1758 |
| *Megalagrion jugorum* | Perkins, 1899 |
| *Orthetrum cancellatum* | Linnaeus, 1758 |
| *Orthetrum coerulescens* | Fabricius, 1798 |
| *Platycnemis pennipes* | Pallas, 1771 |
| *Pyrrhosoma nymphula* | Sulzer, 1776 |
| *Somatochlora arctica* | Zetterstedt, 1840 |
| *Somatochlora metallica* | Vander Linden, 1825 |
| *Somatochlora septentionalis* | Hagen, 1861 |
| *Sympetrum danae* | Sulzer, 1776 |
| *Sympetrum dilatatum* | Calvert, 1892 |
| *Sympetrum flaveolum* | Linnaeus, 1758 |
| *Sympetrum fonscolombii* | Selys, 1840 |
| *Sympetrum nigrescens* | Lucas, 1912 |
| *Sympetrum sanguineum* | Müller, 1764 |
| *Sympetrum striolatum* | Charpentier, 1840 |
| *Tetragoneura cynosura* | Hagen, 1861 |